

EXPERIMENTAL STUDIES ON THE
NATURE OF SPECIES

I. EFFECT OF VARIED ENVIRONMENTS ON
WESTERN NORTH AMERICAN PLANTS

CLAUSEN • KECK • HIESEY

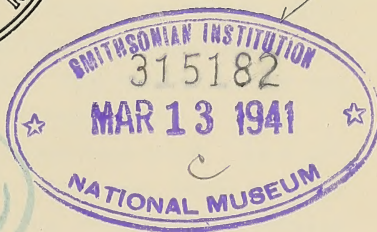
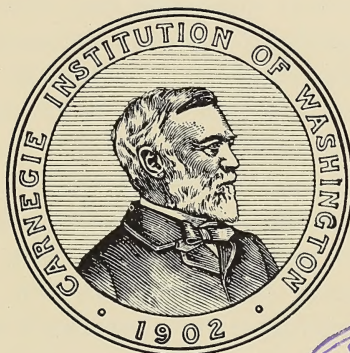
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EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES,

I. EFFECT OF VARIED ENVIRONMENTS ON WESTERN NORTH AMERICAN PLANTS

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CARNEGIE INSTITUTION OF WASHINGTON PUBLICATION NO. 520
WASHINGTON, D. C.

1940

[This book was first issued July 12, 1940]

GIBSON BROTHERS, INC.
STANDARD ENGRAVING CO.
WASHINGTON, D. C.

PREFACE

A unique opportunity to improve the established technique of interpreting the natural units of plants has existed ever since new tools for taxonomic study have become available in recent years. The new methods include experiments with living plants, integrated with cytogenetic analysis. As contrasted with the purely observational and descriptive approaches of the past, experimental methods are laborious and time-consuming; therefore improvement in classification is slow. Nevertheless, it is now clear that the relationships between plants can be determined much more accurately by applying the experimental methods, and from the facts already brought to light new concepts of the organization of the plant kingdom are coming into view.

Dr. Harvey Monroe Hall (1874–1932), who had the gift to grasp fundamental biological problems and attack them by diverse means, was a pioneer in endeavoring to improve existing methods of plant taxonomy. He was led to recognize the need for a better understanding of relationships through his work on large, polymorphic species. A knowledge of the capacities of a plant to adjust itself to varying environments was especially desirable in species with intergrading forms occupying a series of habitats. This led Hall to undertake a series of experiments in which plants were transferred from one environment to another in order to test their capacity for modification.

The investigations of the present report have emanated from the program that Hall carried on for a decade until his untimely death. Many of the plants discussed in this volume were collected and studied by him, and the transplant stations at which these experiments have been conducted were established through his initiative. It is a matter of deep regret that Hall was unable to see the completion of the investigations which he inaugurated.

A strategic field was selected for this experimental work. In California, extremes in altitude ranging from below sea level to high alpine peaks occur in proximity, and marked contrasts in rainfall are found as one travels from the humid region of the Coast Redwoods, across dry valleys and wet mountain meadows to the desert beyond. The native flora is as complex as the dissected topography and varied climates over which it is spread. In a transect across

the central part of the state, ranging in altitude from sea level to over 3000 meters, above timber line, Hall found an ideal natural setting for these investigations.

It was inevitable that the investigations should turn to the larger biological problems. Data became available for the consideration of the nature of species, and of the barriers separating them, as the relations between plants and their environment were studied experimentally. These led to cytological and genetical investigations, coupled with field studies. The results from these diverse approaches have thrown new light on fundamental principles regarding the nature and evolution of natural units and their distribution.

This volume deals with the experiments in transplanting perennial wild plants to different natural environments, from those initiated by Hall in 1922, through the years to 1938; most of the data employed were systematically gathered over a four-year period, 1934 to 1937. As much evidence as possible has been added from our cytological and genetical studies of these materials. This is necessary in order to clarify the relation between heredity and environment, and to lay the foundation for the elucidation of principles relating to the organization of plant species, as set forth in chapter XII.

This volume represents closely coordinated research by the three authors. Since 1932, Hiesey has carried the main responsibility for the execution of the transplant experiments and the recording of the data. All have contributed to the analyses of these, with the greater share of the genetic and cytologic investigations falling to Clausen, and the systematic and nomenclatorial questions to Keck. All the conclusions in this volume are the cooperative work of the three authors.

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June 10, 1939

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GLOSSARY OF IMPORTANT TERMS

Cenospecies, a term proposed by Turesson (1922*b*, 1929) to denote a group of plants "of common evolutionary origin, so far as morphological, cytological and experimental facts indicate." They are so related that they may exchange genes among themselves to at least a limited extent through hybridization. Much morphological dissimilarity and partial genetic incompatibility may exist among members of a *cenospecies*. More than one taxonomic species and more than one *ecospecies* are usually involved in a *cenospecies*, which sometimes corresponds to a taxonomic section or a genus.

Clone, all the asexual propagules derived from one individual; *clone member*, a single propagule of a clone.

Ecospecies, Turesson's term (1922*b*, 1929) used to denote a group of plants within the *cenospecies* whose members are able to interchange their genes without detriment to the offspring. *Ecospecies* are separated from one another by internal barriers that prevent such free interchange. They may or may not correspond to the Linnaean taxonomic species.

Ecotype, a group of biotypes within an *ecospecies*, that is, "the product arising as a result of the genotypical response of an *ecospecies* to a particular habitat" (Turesson, 1922*a*, 1922*b*). It is characterized by its fitness for a particular environment within the range occupied by the *ecospecies* as a whole. One or more *ecotypes* may be contained within one *ecospecies*; if these are morphologically distinguishable, we classify them as taxonomic subspecies.

Modification, a nonheritable morphological or physiological change induced in an individual as a result of change in environment, that is, a different phenotype of the same genotype.

Race, a local, genetically distinct aspect of a species.

Transplant, an individual used in the varied-environment experiments; such individuals are *transplanted*.

I

INTRODUCTION

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PURPOSE AND PRINCIPLES

The object of the varied-environment experiments has been to discover principles that govern the distribution of plants and their organization into natural units. In pursuing this objective we have studied the capacity of plants to adjust themselves to a series of contrasting habitats, and the interplay between heredity and environment.

From the beginning of the investigations several general facts have been realized. First, many plants are grouped by relationship into complexes of diverse content but of a common hereditary pattern. Second, such complexes are widely distributed through many environmental conditions. Third, there is a correlation between the gross morphology of plants and features of their natural habitats. Familiar examples of the last point within single species are the tall plants of the lowlands as contrasted with the dwarfs of alpine regions, plants with coarse leaves found in hot, sunny situations and those with broad, thin leaves found in shade, the succulents of xeric habitats; and so on. What is the nature of such diversity within a species or a species complex? Are the variations non-heritable and therefore reversible modifications, or do they represent heritable race differences?

In seeking to answer these questions it is obvious that a dual approach is necessary: first, to study uniform heredity in varied environments, and second, varied heredity in a uniform environment. Our results will be of no scientific value if these factors are confused. The appearance or phenotype of the plant at any time is, of course, the result of the interplay between heredity and environ-

ment; therefore, no more than one of these sets of variables may be compared at one time.

In studying the effects of varied environments the unit of prime importance is the individual. The study of individuals propagated as clones is much more fruitful than that of many times the number of individuals of varying heredity. Therefore, the experiments recounted in the following pages have not been concerned with large numbers of plants, but with reasonably large samples of accurately documented individuals.

On the other hand, if the primary objective is the study of hereditary diversity within a species, larger samples of the natural populations must be taken for comparison in uniform environment. However, more information on diversity in heredity and reaction can be gained if, by clonal division, such samples are studied not only in one but in several different environments. This permits two series of comparisons: first, between plants of unlike heredity in uniform gardens, and second, between genetically identical materials in different environments.

The unit of greatest interest to students of evolution is the species. Species are not homogeneous units; they are complex aggregations of individuals. Some species are able to maintain themselves in a great range of environmental conditions, and over a large geographic area; others are restricted to local niches outside of which they cannot successfully compete for existence. Obviously, there must be some fundamental difference between species of wide and of narrow distribution. For this reason both kinds of species have been included in these studies. Moreover, in order to investigate the composition of a species of wide distribution, it is essential to study samples from as many kinds of environment within its range as possible. For this reason we have aimed particularly to include in the experiments representatives of altitudinal races of species that occur in a transect across California.

By comparing plants not only in one uniform environment but also in a series of environments at different altitudes, it has been possible to gain a comprehensive picture of the composition of species, both those of wide and those of narrow distribution. Aspects of polymorphic species that have long perplexed botanists have been greatly clarified. The following chapters abound in this kind of comparison.

The heredity of plants may be compared in several ways. One of these is indirect, and consists in comparing morphological and physiological characters in a uniform environment. The differences that remain under such conditions are hereditary. Another way is direct, and consists in crossing plants and studying the recombination of their genes. This makes possible an approximate analysis of the genetic systems of related ecotypes and ecospecies. A third way of comparing heredity is through cytological analysis. In its simplest form this method consists in counting the chromosomes of various races and populations of which the group under study is composed. When differences occur, the attempt is made to correlate them with either the morphology or the distribution of the race complex, or both. An analysis of a little deeper significance is the cytogenetic. It consists in comparing the homology of the chromosomes of various forms by bringing them together in a hybrid and analyzing their mode of conjugation.

So far as possible, all these methods have been employed in the studies presented in the following pages. The morphological comparisons are, of course, of first importance in classification, but the cytological and genetical tests are the more conclusive indicators of relationship. The combined results from all the evidence show how genetic relationship may be linked to morphological characters, and how these, in turn, may be correlated with distribution in different environments. It follows that the plants used in such studies must of necessity represent natural populations.

By following these general principles, it has been possible to depict in much clearer detail than formerly the nature and composition of plant species, and their relation to environment. Many questions still remain unsolved, but many features of species composition that are of general significance in the plant kingdom are now evident.

HISTORY

A number of years ago Kerner (1891) and Bonnier (1895, 1920) observed the differences between alpine and lowland plants of the same or related species, and studied them experimentally. Both investigators transplanted lowland plants to high altitudes and vice versa for the purpose of comparing them in later years. Their objective was to determine whether the differences between alpine

and lowland plants of the same or related species are due to environment or to inherent characteristics. A further discussion of their results is presented in chapter XI.

Inspired by the work of Bonnier, Clements began a series of varied-environment experiments at Pikes Peak, Colorado, along a transect ranging in altitude from 1830 to 4270 m. In 1918 H. M. Hall became associated with Dr. Clements at Pikes Peak, and for three years he was an active co-worker in the Colorado experiments. The original objectives of this project were: "(1) to determine the extent to which species and their variads could be modified by habitat factors; (2) to test the nature and value of the criteria employed in taxonomy; and (3) to contribute to a knowledge of the rôle of environment in evolution" (Carnegie Institution of Washington Year Book No. 24, 1924-1925, p. 314). In 1922 Hall began investigations along these lines in California, where certain natural advantages were offered, especially in the more varied topography and climate. These investigations have been in continuous development since. One report was made on them by Hall (1932).

Beginning about the year 1920, Turesson (1922*b*) in southern Sweden developed the standard-environment transplant method for the comparison of races of widely distributed species in one uniform environment. This led to the concept of ecotypes. The investigations to be described in the following chapters represent a combination of the varied- and the standard-environment methods, together with that of cytogenetic analysis.

TRANSPLANT STATIONS

The varied-environment experiments have been conducted along a California transect extending from the Pacific Ocean at Point Montara, San Mateo County, across the Santa Cruz Mountains to Stanford University, Santa Clara County, thence eastward across the Inner Coast Range, the San Joaquin Valley, and the Sierra Nevada to the Great Basin at Benton, Mono County. A relief map and diagrammatic profile, indicating locations and altitudes of garden activities along this transect, are shown in figure 1.

During the first years of the experiments (1922-1924), small detached areas along this transect were developed at the coast and in the Sierra Nevada. As work progressed, the necessity for centralizing these scattered plots into fewer and better-cared-for units

became evident. Accordingly, in 1927 the development of five stations at different altitudes was proposed. These were at Montara, Stanford, Mather, and Timberline.

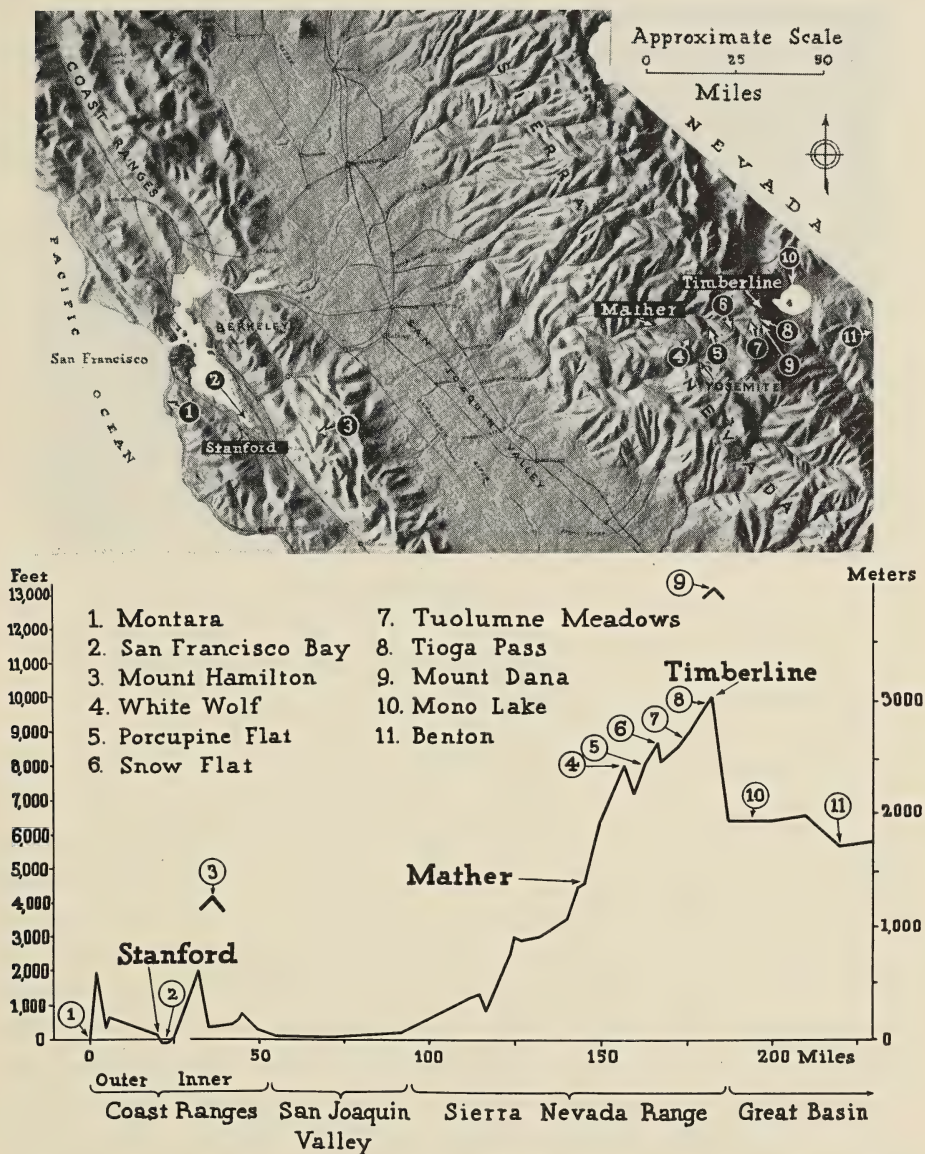


FIG. 1. Above: relief map of the central part of California, showing location of the Stanford, Mather, and Timberline stations and points of interest along the transect. (Photograph of a relief model taken by permission of the Department of Geology, Stanford University.) Below: profile showing elevations of these locations. Corresponding numbers on the relief map and on the profile refer to the same points.

Berkeley, Mather, Timberline, and Benton. At some of these stations a series of gardens differing in light and moisture were planned. Thus two sets of variables were involved, (1) altitudinal differences between stations, and (2) differences in light and moisture at one altitude. Most of the plots outlined were realized and some data have been accumulated from them.

The maintenance of so many gardens proved to be too large an undertaking for a small staff. The gardens at Montara and Benton, which were most restricted in their uses and most difficult to maintain, were therefore given up. The functions of the Montara station had been taken over in large part in 1929 by the new central laboratory and gardens at Stanford, into which, also, the materials that had been growing at Berkeley were moved. The Benton station had been used at its inception for experiments on the rubber content of *Chrysothamnus* species by Dr. Hall, but the alkalinity and excessive aridity caused very heavy losses in most of the species grown there. Furthermore, poor roads and the long distance from base stations made its maintenance expensive.

Consequently, past experience was utilized in planning and adopting a new and simplified plan of garden development in 1933. The most important documentation of results followed the changes of that time. In figure 2 a diagrammatic representation of the present placement of gardens is given.

During the early years of the work most of the operations were performed directly in the field; that is, plants to be moved from one altitude to another were dug and transplanted immediately into their new habitat. Losses were heavy, so it was found advisable to establish newly acquired plants in pots at a centrally located station before transferring them into the field at a new habitat. A small nursery was maintained at Berkeley between 1925 and 1929, but since that time greatly improved facilities have been available at the central laboratory at Stanford. Here newly propagated individuals are started under uniform conditions. This favors more consistent and comparable results at the transplant stations.

The stations and gardens described below may be located with respect to each other by consulting figure 1.

BERKELEY. Elevation 12 to 90 m. (40 to 300 ft.). Some early transplants were grown in a lot adjacent to the residence of Dr. Hall, at 90 m. elevation, but the principal plot was located on Uni-

versity of California land in West Berkeley, known as the Schmidt Tract. This served as a base of operations for transplant work between 1926 and 1929.

STANFORD. Elevation 30 m. (100 ft.). Since 1929, the central laboratory of the Division of Plant Biology of the Carnegie Institution of Washington, located on the Stanford University campus near Palo Alto, has been the base of operations for the transplant experiments. A view of the gardens is shown in figure 3.

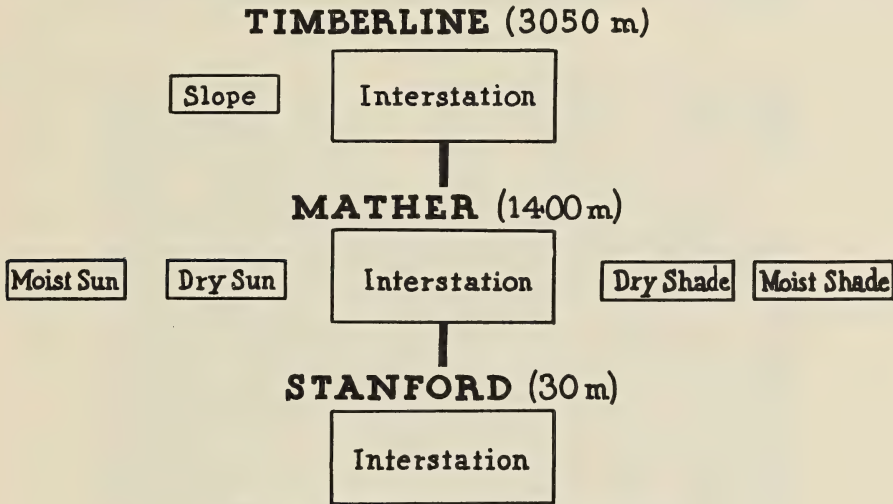


FIG. 2. Diagram showing plan of gardens

The climate at Berkeley and Stanford is mild, typical of the coast region of central California, where conditions are favorable for the growth of many species almost the entire year. In contrast with conditions at the Sierran stations, snows are practically unknown except for occasional falls in the surrounding Coast Ranges. Frosts may occur between the first part of November and the middle of March in average years. The summer and autumn months are commonly very dry, and rains are almost entirely confined to the winter and spring months. Winter frosts are more frequent and severe at Stanford than at Berkeley. Because of its proximity to San Francisco Bay and the ocean beyond, Berkeley is subject to more fog but to less chilling temperatures than Stanford. The climates of Berkeley and Stanford are, nevertheless, quite comparable. Temperature and precipitation curves constructed from U. S. Weather Bureau data for Palo Alto are given in figure 4.



Timberline, elevation 3050 m.



Mather, elevation 1400 m.



Stanford, elevation 30 m.

FIG. 3. VIEWS OF TRANSPLANT GARDENS

Characteristic tree species native at Stanford include *Quercus agrifolia* Née, *Q. Douglasii* H. & A., *Q. lobata* Née, *Umbellularia californica* Nutt., and *Aesculus californica* Nutt. Among the commoner broad-sclerophylls of the chaparral are *Adenostoma fasciculatum*

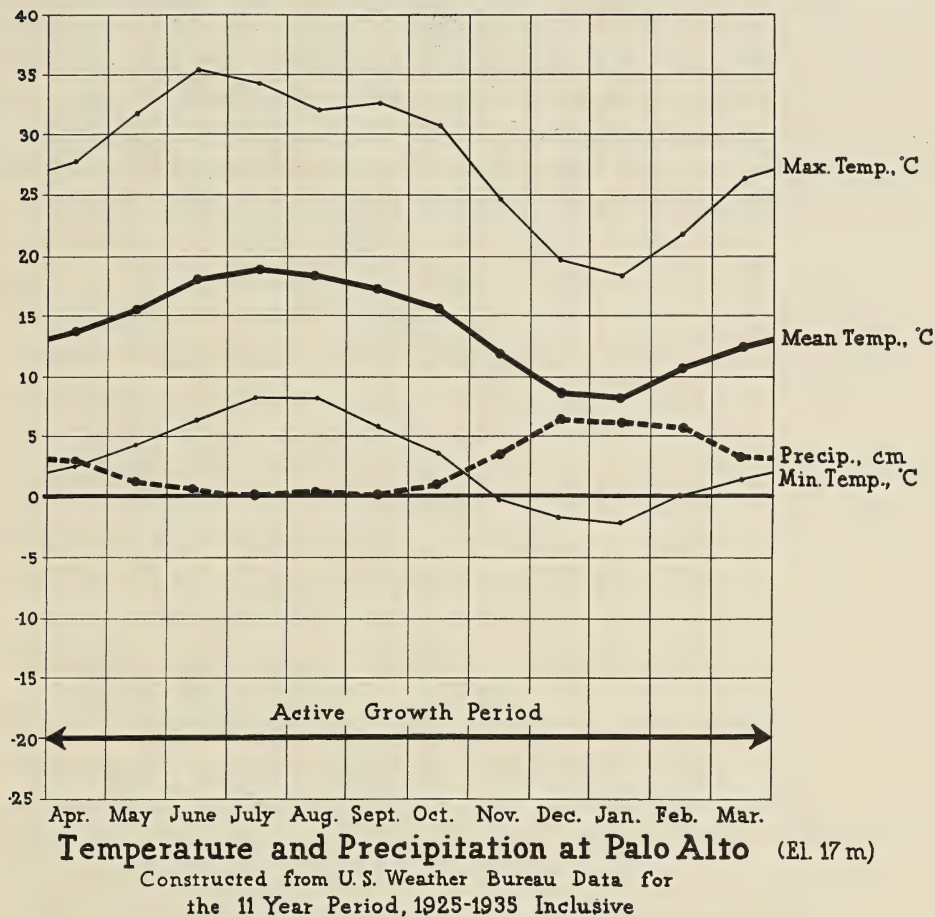


FIG 4. Weather data from Palo Alto, near the Stanford gardens.

Max. Temp., average of the highest monthly temperatures. *Mean Temp.*, average of the mean monthly temperatures obtained from daily readings. *Precip.*, average monthly precipitation. *Min. Temp.*, average of the lowest monthly temperatures. Average annual precipitation 31.7 cm. (12.49 in.). No snowfall, except traces in 1931 and 1932.

H. & A., *Photinia arbutifolia* Lindl., *Rhamnus californica* Esch., and *Quercus durata* Jeps. Other common shrubs include *Rhus diversiloba* T. & G., *Artemisia californica* Less., and *Ceanothus cuneatus* (Hook.) Nutt., while there are many drought-enduring herbs such as *Artemisia Douglasiana* Bess. and the tarweeds, including *Hemizonia*

luzulaefolia DC. In the springtime a rich flora of ephemeral annuals colors the landscape, among which the predominant flower is very often the longer-lived California poppy, *Eschscholtzia californica* Cham.

In the Santa Cruz Mountains, within ten kilometers of the Stanford station, the average annual rainfall is 75 to 100 cm. per year, far in excess of the precipitation at Stanford with its mere 25 to 40 cm. The composition of the flora consequently undergoes a rapid change as one approaches the mountains, where such moisture-loving species as the Redwood, *Sequoia sempervirens* (Lamb.) Endl., occur.

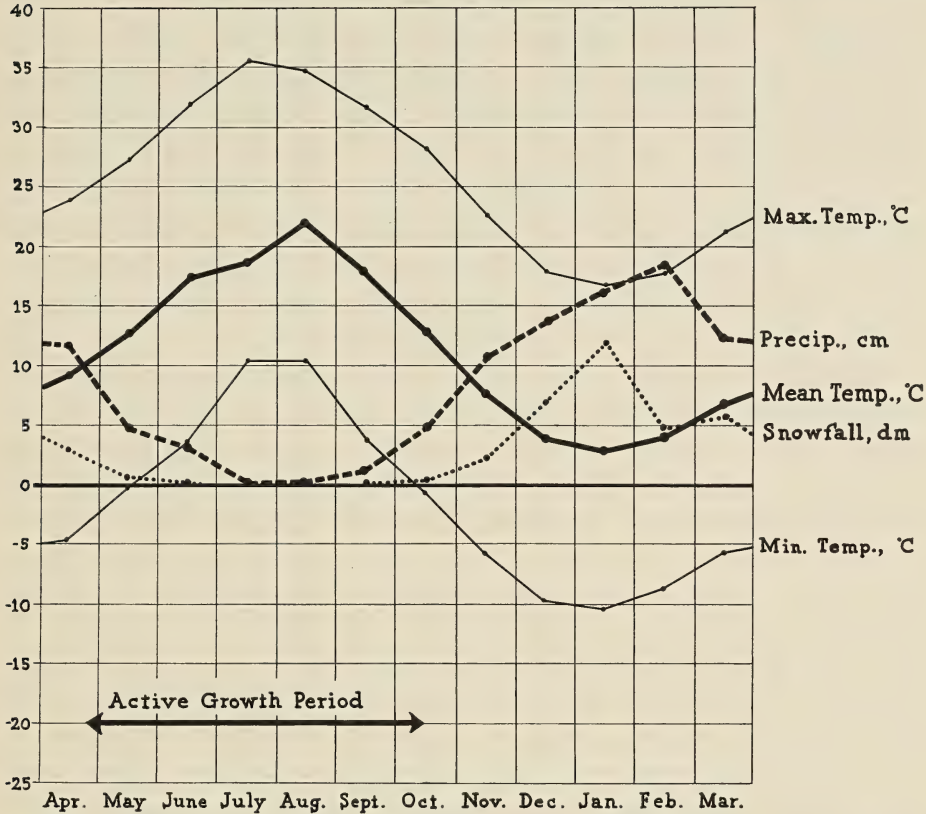
MATHER. Elevation 1400 m. (4600 ft.). This station is situated in the Stanislaus National Forest, Tuolumne County. The U. S. Forest Service has granted to the Carnegie Institution of Washington for experimental purposes free use of an area covering forty acres. The use of an adjacent area for similar purposes has been granted by the city of San Francisco. A general view of some of the transplant gardens is shown in figure 3.

Spring weather begins ordinarily the first part of April, at which time most snows have melted, although frosts occur until the first part of June. The summers are mild, usually with warm days and cool nights, and are mostly free of rain. The autumn months are typically cool and dry. The first snows usually appear in October or November, and the heaviest ordinarily do not exceed two or three feet in depth. Temperature and precipitation curves constructed from U. S. Weather Bureau data for Lake Eleanor, located ten kilometers north of Mather, are given in figure 5. This locality has nearly the same elevation as Mather and a similar climate.

Mather is in the Transition life zone of C. H. Merriam's classification (1898). Characteristic species include *Pinus ponderosa* Dougl., *Libocedrus decurrens* Torr., *Quercus Kelloggii* Newb., *Q. chrysolepis* Liebm., *Arctostaphylos mariposa* Dudley, and *Ceanothus integerrimus* H. & A. Some trees of *Pinus Lambertiana* Dougl. and *Abies concolor* Lindl. & Gord. occur, species mostly distributed at higher elevations. A few individuals of *Pinus Sabiniana* Dougl. and *Torreya californica* Torr. intrude from lower altitudes.

Mather station has been in use since 1922. In the first years of the transplant work, many detached plots varying in moisture, shade,

and slope exposure were used. Individual reciprocal transplants¹ were scattered in forests and in meadows. Subsequent centralization into fewer and larger gardens was a necessary consequence of



Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar.

Temperature and Precipitation at Lake Eleanor (El. 1400 m)

Constructed from U.S. Weather Bureau Data for
the 11 Year Period, 1925-1935 Inclusive

FIG. 5. Weather data from Lake Eleanor, near Mather transplant station.

Max. Temp., average of the highest monthly temperatures. *Precip.*, average monthly precipitation (rainfall plus snowfall). *Mean Temp.*, average of mean monthly temperatures obtained from daily readings. *Snowfall*, average monthly snowfall. *Min. Temp.*, average of the lowest monthly temperatures. Average annual precipitation 97.7 cm. (38.45 in.).

the difficulty in maintaining these small, semiorganized units. When plants were moved from these original areas to the new gardens, their identity was very carefully preserved.

WHITE WOLF. Elevation 2460 m. (8090 ft.). Situated along the

¹For explanation of reciprocal transplants see pp. 15-16.

Tioga Road, Yosemite National Park. A few small plots were developed adjacent to moist meadows and in wooded areas partly shaded by *Pinus Murrayana* Balf. All plants which survived were moved either to Mather or to Timberline in 1929.

PORCUPINE FLAT. Elevation 2500 m. (8200 ft.). Located along Tioga Road, Yosemite National Park. Scattered plots similar to those at White Wolf were established for reciprocal transplants. All surviving cultures were moved to Mather or Timberline in 1929.

SNOW FLAT. Elevation 2650 m. (8700 ft.). Near Mount Hoffmann, Yosemite National Park. Transplants (mostly Dodecatheons) were grown here in the wet meadows, some of which were partly shaded by *Pinus Murrayana* Balf. or *P. monticola* Don. All surviving plants were moved to Timberline in 1929.

TUOLUMNE MEADOWS. Elevation 2620 to 2770 m. (8600 to 9100 ft.). Situated nine miles west of Tioga Pass, Yosemite National Park. These meadows were the center of extensive operations during the earlier years of the experiments, when a number of plots were established. At Moraine Flat, on the northeast edge of Tuolumne Meadows, plantings were made in plots differing in moisture and in light. Here natural shade was supplied by *Pinus Murrayana* Balf., and sites differing in moisture were obtained by selecting plots on relatively dry, well-drained slopes and in moist swales. Other local areas utilized in Tuolumne Meadows included: Soda Springs, Lambert Dome, a meadow on the banks of the Lyell Fork of the Tuolumne River, and plots along the Dana Fork. All the transplants surviving at Tuolumne Meadows were moved to Timberline in 1929.

TIOGA PASS. Elevation 3030 m. (9940 ft.). Small plantings were made at the Pass. Some data of interest accumulated from them. In 1929 the survivors were transferred to Timberline.

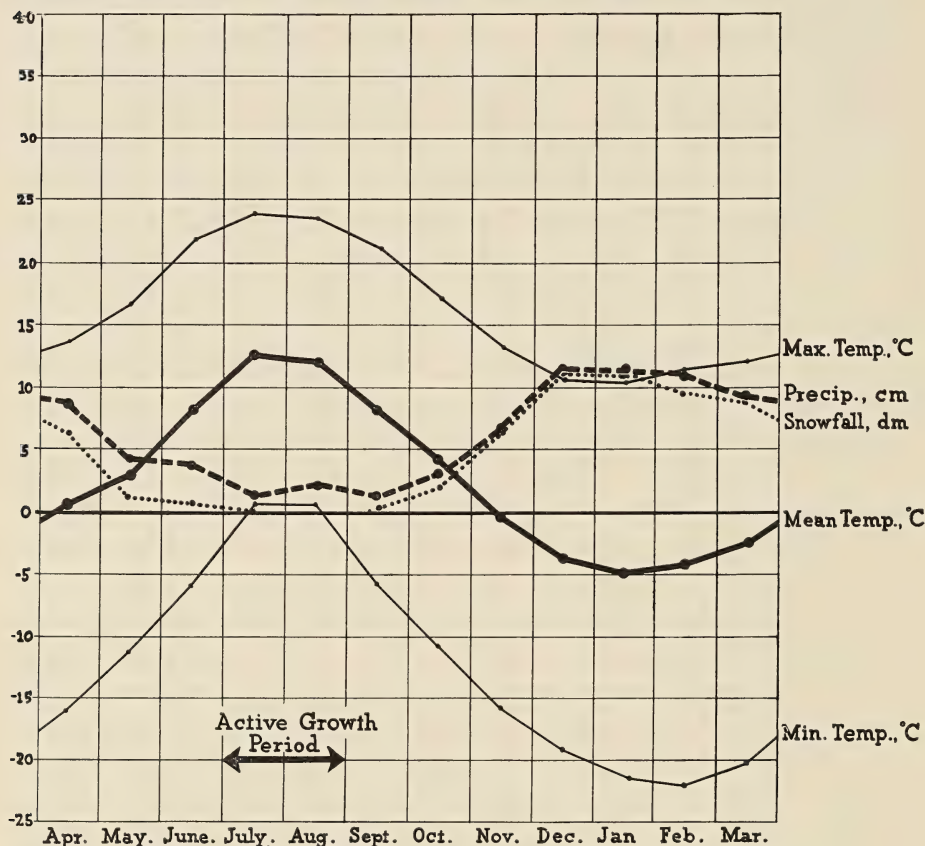
TIMBERLINE. Elevation 3050 m. (10,000 ft.). A view of the interstation garden in Slate Creek Valley is shown in figure 3. The station site was selected after a careful study of different locations in the Sierra Nevada. It lies within land now included in the Harvey Monroe Hall Natural Area,² Mono County. The major

²This area, of approximately nine square miles, in the Mono National Forest, has been set aside by the U. S. Forest Service in cooperation with the Carnegie Institution of Washington as a natural reserve for the purpose of conducting scientific research. The area adjoins the eastern boundary of Yosemite National Park.

part of this area is in Slate Creek Valley, surrounded by peaks of the Sierran crest reaching heights of 3350 to 3800 m. (11,000 to 12,550 ft.). Small glaciers occur on the shady sides of some of the crests, and snow banks near the garden usually persist well past the middle of July. Winter snows on the valley floor do not ordinarily melt before June 20 to July 1, and the first snowfall of the season is normally expected the latter part of September. During the entire year there are but three to six weeks of frost-free weather, and at no time is there assurance that frosts will not occur. In midwinter, snows four to six meters in depth may accumulate. Thus the rigorous climate at Timberline is in marked contrast to the mid-Sierran weather at Mather, and to the mild coastal conditions at Berkeley and Stanford. Temperature and precipitation curves constructed from U. S. Weather Bureau data for Ellery Lake, five kilometers from Timberline station at 2890 m. elevation, are given in figure 6. The climate at Ellery Lake is similar to that at Timberline station, but at Timberline the winters are somewhat more severe because of the higher elevation. The flora in the two localities is much the same.

Species native in the vicinity of Timberline station are typically alpine. Although large trees of *Pinus Murrayana* Balf. and an association of plants characteristic of lower elevations grow in the immediate vicinity of the station on a warm slope of southern exposure, the location is close enough to actual timber line to justify the station name. Tree line is not sharply defined in this region and varies from 3140 to 3300 m., according to exposure. It is formed by scrub timber of *Pinus albicaulis* Engelm., but scattered specimens of *Tsuga Mertensiana* (Bong.) Sarg., *Juniperus occidentalis* Hook., and prostrate specimens of *J. communis* L. grow in the area. Local conditions, such as exposure to wind, sun, and cold-air drainage, are factors of relatively greater importance in determining plant distribution than at Stanford and Mather. In addition to the conifers mentioned, typical plants of this area in the Arctic-Alpine life zone include: *Phegopteris alpestris* Hoppe, *Phleum alpinum* L., *Salix petrophila* Rydb., *Oxyria digyna* (L.) Hill, *Rhodiola rosea* L., *Par-nassia palustris* L., *Saxifraga nivalis* L., *Sibbaldia procumbens* L., *Potentilla fruticosa* L., *Cassiope Mertensiana* Don, *Vaccinium caespitosum* Michx., *Pedicularis groenlandica* Retz., *Veronica alpina* L., *Aster Andersonii* Gray, and *Raillardella argentea* Gray.

Timberline station was developed in 1929. It was made accessible through the aid of the U. S. Forest Service, by the construction of a road approximately one mile in length connecting the station site with roads leading to main highways. Mr. W. M.



Temperature and Precipitation at Ellery Lake (E1.2890m)

Constructed from the U.S. Weather Bureau Data for
the 11 Year Period, 1925-1935 Inclusive

FIG. 6. Weather data from Ellery Lake, near Timberline station.
Legends as in figure 5. Average annual precipitation 74.1 cm. (29.19 in.).

Maule, Forest Supervisor of Mono National Forest, aided in many ways during its development.

GARDENS DIFFERING IN MOISTURE AND LIGHT. In addition to growing the plants at different altitudes, it was considered advisable to test the effect of local variations in environment at one station. The object of this phase of the experiments was to compare the

modifications induced by local differences with the modifications brought about by transplanting to different altitudes. For this purpose Hall originally utilized small natural plots of varying exposure, some shaded by trees, others in sunny places, some on dry slopes, and others in moist swales. Much effort was spent in establishing such plots at Mather and at Tuolumne Meadows, but, because of the difficulties in maintaining such gardens, these proved to be generally unsuccessful.

In more recent years (i.e., since 1933) these have been abandoned except for a series at Mather. Here four plots were maintained, two of which were shaded by lathhouses with the laths spaced one-quarter of an inch apart, and placed six and one-half feet above the ground. The two corresponding plots were placed in the full sun. One shade and one sun plot were located well within a meadow, and were kept moist by irrigation. Two corresponding gardens were placed on a near-by dry slope and were never irrigated. These four plots will be collectively referred to as the "water-light" gardens, consisting of a moist sun, moist shade, dry sun, and a dry shade garden. Three of these can be seen in the view of the Mather gardens in figure 3—the moist shade on the extreme left, the dry sun in the foreground, and the moist sun beyond it. The dry shade garden, not included in the photograph, was to the right of the dry sun plot. Quadruplicate plantings of selected clones in limited number were set in the four water-light gardens in addition to the interstation garden series.

PLANT MANIPULATIONS

During the course of the work, several methods have been employed in the handling of plants:

RECIPROCAL TRANSPLANTS. This method was developed by Clements and Hall (1918) at Pikes Peak, Colorado, and was continued by Hall in his work in the California transect. It consisted of digging an individual plant at one altitude and moving it to another elevation, making, at the same time, a reciprocal exchange in the reverse direction. To insure an exact reversal of habitats, the transplants were set into the same holes from which their reciprocals were dug. At the time of transfer, herbarium specimens, notes, and sometimes photographs were taken of the two individuals in

order to provide a descriptive record of their characteristics at the beginning of the experiment.

The transplants were labeled in their new positions by stakes marked with the experiment number, and the transfer was systematically recorded. To insure against damage or disturbance of the stakes, charts were made showing location of the plants with reference to each other and to garden boundaries or natural landmarks. Contamination from surrounding native plants, and from seedlings of the transplants themselves, was prevented by careful yearly weeding. In the years following, herbarium specimens and notes were taken of the plants for comparison with the original records. In this way, changes which might have taken place in morphological characters following transplanting could be studied.

This method, while simple and logical, was difficult to apply. As the number of experiments increased, transplants became scattered through the mountains without adequate protection from campers and grazing animals. Record-taking and curating became laborious and costly. Moreover, casualties due to shock from this direct transplanting were so heavy that the actual data obtained were quite fragmentary. However, some evidence of interest is on hand as a result of these experiments.

SOD TRANSPLANTS. Because losses were heavy with reciprocal transplants, Hall attempted some work with sod transplants in 1923-1924. Instead of exchanging bare-rooted individuals as reciprocals, sods containing the desired species were transferred. These were soon abandoned because of the impracticability of transporting heavy balls of earth over mountain roads, and because of uncertainty as to the identity of individual plants. No further reference will be made to these.

CLONE TRANSPLANTS. This method, used by Bonnier in his experiments in the Alps and in the Pyrenees, was further developed by Clements and Hall (1919) under the name "variation transplants." This has proved to be the most satisfactory technique and is the only one that was extensively used. A plant selected for experiment is dug, and its roots are washed free from soil to insure the taking of only a single individual. At the time of digging, a herbarium specimen is taken, the individual is assigned an experiment number, and appropriate entries are made in the records giving information

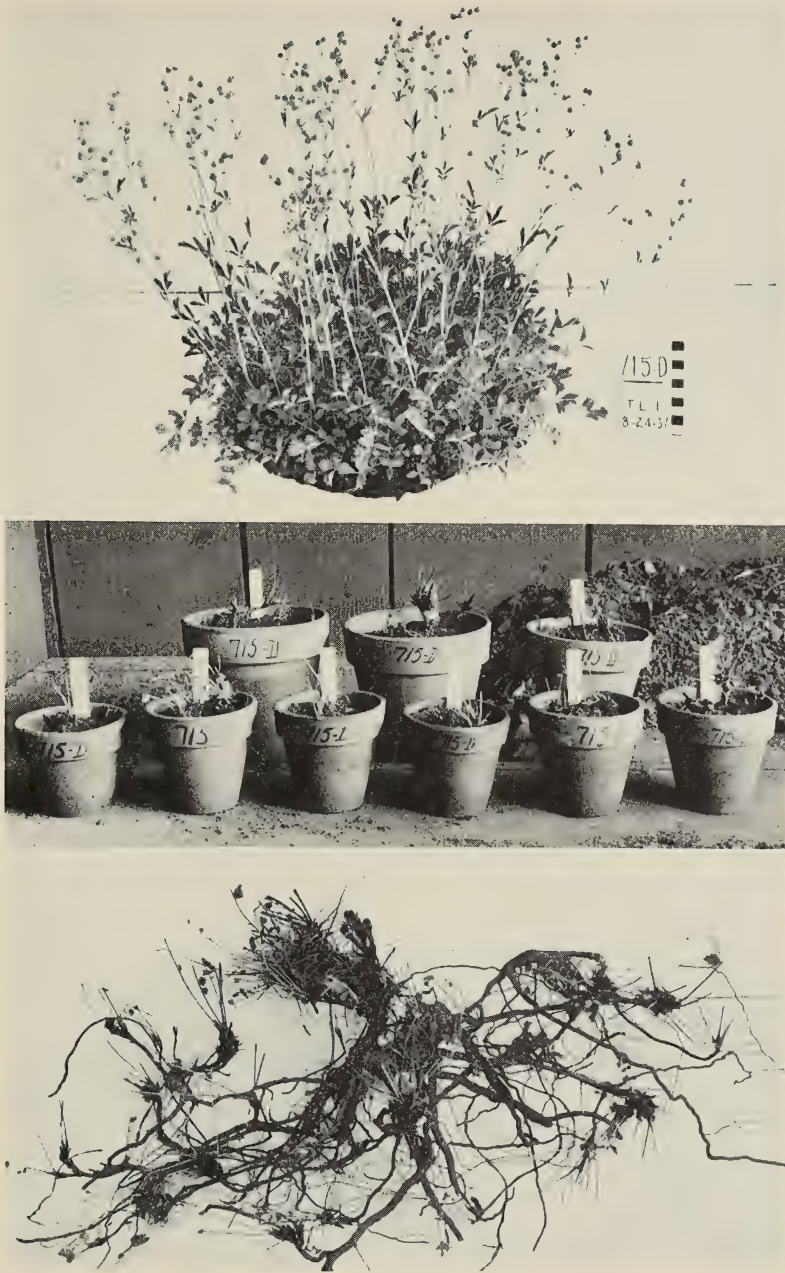


FIG. 7. Method of clone transplanting.

Below: root of an individual of *Potentilla glandulosa* washed free from soil after it was dug in its native habitat at Tuolumne Meadows, Yosemite National Park, September 14, 1926. *Center:* same individual divided into propagules and potted at Berkeley a few days later. *Above:* a clone member growing in a transplant garden at Timberline, August 24, 1937. The black and white scale is 10 cm. long and 1 cm. wide. (The same scale is used with other portraits in this volume.)

such as date, exact location, morphological characteristics, and brief descriptions of the habitat. Plants thus treated are then packed in moist sphagnum, wrapped tightly, and transferred to the base station for propagation. Here they are divided vegetatively into as many parts as are required, or as many as the strength of the plants permits. Each propagule is potted, labeled with its number, and established in a nursery, usually at the base station. When the clone members become strong enough, they are planted in the gardens at the different stations. Ordinarily, transplants dug in the summer of one season are divided and ready for transfer to garden plots the following spring. The method is illustrated in figure 7.

The transplants are set in gardens at the stations and cultivated to prevent contamination by the native flora or by their own seedlings. Each clone member is marked by a stake bearing the individual plant number. As a further precaution, the plants in the gardens are charted.

Following transplanting, yearly records are taken from each of the divisions, including a herbarium specimen, notes, and sometimes photographs. From 1934 to 1937 detailed data from each clone member were tabulated on printed forms. Such permanent records make it possible to compare clone members of a given individual growing in different habitats for indefinite periods of time.

MATERIALS

In the early phases of the investigations, a great many species representing a number of families were transplanted. Many proved unsuitable for the work, and heavy losses resulted. It became obvious that it was necessary to restrict the investigations to those species which were especially well adapted for transplanting. The greatest amount of evidence has been obtained from *Potentilla*, *Zauschneria*, *Achillea*, and *Artemisia*, but considerable supplementary evidence is on hand from other groups. Well over a thousand individuals have been used in the experiments.

A list of the species that were tried is given below. Those marked with an asterisk (*) have yielded sufficient data to be discussed in this report. From the others too little information has been obtained to warrant further consideration.

OPHIOGLOSSACEAE

- | | |
|--------------------------------|-------------------------------|
| Botrychium Lunaria (L.) Swartz | Botrychium simplex E. Hitchc. |
| B. silaifolium Presl | |

POLYPODIACEAE

- | | |
|---------------------------------|------------------------------------|
| Athyrium americanum (Butters) | Polystichum munitum (Kaulf.) Presl |
| Maxon | Pteridium aquilinum (L.) Kuhn |
| Dryopteris arguta (Kaulf.) Watt | and var. lanuginosum (Bong.) Fern. |

GRAMINEAE

- | | |
|--------------------|---------------------------------------|
| *Phleum alpinum L. | *Sitanion Hystrix (Nutt.) J. G. Smith |
|--------------------|---------------------------------------|

CYPERACEAE

- *Carex festivella Mcke.

JUNCACEAE

- | | |
|------------------------|------------------------|
| Juncus balticus Willd. | *Juncus Parryi Engelm. |
|------------------------|------------------------|

LILIACEAE

- | | |
|---------------------------------------|------------------------------|
| Allium validum S. Wats. | Zygadenus venenosus S. Wats. |
| Trillium chloropetalum (Torr.) Howell | |

IRIDACEAE

- | | |
|--------------------------|-------------------------------|
| Iris missouriensis Nutt. | *Sisyrinchium bellum S. Wats. |
|--------------------------|-------------------------------|

SALICACEAE

- | | |
|--------------------------|-------------------------|
| Salix orestera Schneider | Salix sitchensis Sanson |
|--------------------------|-------------------------|

POLYGONACEAE

- | | |
|-------------------------------|------------------------------|
| Eriogonum fasciculatum Benth. | Eriogonum nudum Dougl. |
| E. incanum T. & G. | Polygonum bistortoides Pursh |
| E. latifolium Sm. | Rumex salicifolius Weinm. |

CHENOPODIACEAE

- Atriplex confertifolia (Torr. & Frem.) S. Wats.

RANUNCULACEAE

- | | |
|------------------------------|--------------------------------|
| Aquilegia pubescens Cov. | Ranunculus californicus Benth. |
| A. truncata F. & M. | R. orthorhynchus Hook. |
| Delphinium decorum F. & M. | *Thalictrum Fendleri Engelm. |
| Ranunculus Bloomeri S. Wats. | |

CRASSULACEAE

- | | |
|---|--------------------------|
| *Echeveria Cotyledon (Jacq.) Nels. & Macbr. | *Sedum obtusatum Gray |
| | *S. spathulifolium Hook. |

SAXIFRAGACEAE

- | | |
|---|------------------------|
| Philadelphus Lewisii Pursh var. californicus Gray | Ribes montigenum McCl. |
| Ribes divaricatum Dougl. | R. nevadense Kell. |
| | R. Roezlii Regel |

ROSACEAE

- | | |
|--|---|
| <i>Fragaria californica</i> C. & S.
and var. <i>crinita</i> Hall | * <i>Potentilla Drummondii</i> Lehm.
<i>P. flabellifolia</i> Hook. |
| <i>Holodiscus discolor</i> (Pursh) Maxim. | * <i>P. flabelliformis</i> Lehm. |
| * <i>Horkelia Bolanderi</i> Gray ssp. <i>Clevelandii</i> (Greene) Keck | * <i>P. glandulosa</i> Lindl. |
| * <i>H. californica</i> C. & S. | * <i>P. gracilis</i> Dougl. |
| * <i>H. cuneata</i> Lindl. | * <i>P. pectinisecta</i> Rydb. |
| * <i>H. fusca</i> Lindl. | * <i>P. pulcherrima</i> Lehm. |
| * <i>H. tenuiloba</i> (Torr.) Gray | <i>Prunus demissa</i> (Nutt.) Dietr. |
| <i>H. tridentata</i> Torr. | <i>P. subcordata</i> Benth. |
| <i>Ivesia Gordonii</i> (Hook.) T. & G. | <i>Rosa californica</i> C. & S. |
| * <i>Potentilla arguta</i> Lehm. | <i>Rubus leucodermis</i> Dougl. |
| * <i>P. Breweri</i> S. Wats. | <i>Sanguisorba minor</i> Scop. |
| * <i>P. diversifolia</i> Lehm. | <i>Sibbaldia procumbens</i> L. |
| | <i>Spiraea densiflora</i> Nutt. |

LEGUMINOSAE

- | | |
|-----------------------------|---------------------------------|
| <i>Lotus Torreyi</i> Greene | <i>Trifolium monanthum</i> Gray |
|-----------------------------|---------------------------------|

GERANIACEAE

- | | |
|-------------------------------------|--|
| * <i>Geranium caespitosum</i> James | * <i>Geranium Richardsonii</i> F. & T. |
| * <i>G. incisum</i> Nutt. | |

RHAMNACEAE

- | | |
|---|----------------------------------|
| <i>Ceanothus cuneatus</i> (Hook.) Nutt. | <i>Rhamnus californica</i> Esch. |
| <i>C. divaricatus</i> Nutt. | <i>R. crocea</i> Nutt. |
| <i>C. integerrimus</i> H. & A. | |

VITACEAE

- | |
|---------------------------------|
| <i>Vitis californica</i> Benth. |
|---------------------------------|

MALVACEAE

- | |
|--------------------------------|
| <i>Sidalcea reptans</i> Greene |
|--------------------------------|

VIOLACEAE

- | |
|---|
| * <i>Viola adunca</i> Sm. and ssp. <i>oxyceras</i> (S. Wats.) Piper |
|---|

ONAGRACEAE

- | | |
|--|----------------------------------|
| * <i>Epilobium angustifolium</i> L. | * <i>Zauschneria cana</i> Greene |
| * <i>Zauschneria californica</i> Presl | * <i>Z. septentrionalis</i> Keck |

UMBELLIFERAE

- | | |
|--|------------------------------|
| <i>Angelica Hendersonii</i> C. & R. | <i>Osmorrhiza nuda</i> Torr. |
| <i>Ligusticum apiodorum</i> (Gray) C. & R. | |

PRIMULACEAE

- | | |
|-------------------------------------|-------------------------------------|
| * <i>Dodecatheon alpinum</i> Greene | * <i>Dodecatheon Jeffreyi</i> Moore |
|-------------------------------------|-------------------------------------|

GENTIANACEAE

- | | |
|------------------------------|--------------------------------|
| <i>Gentiana simplex</i> Gray | <i>Gentiana Newberryi</i> Gray |
|------------------------------|--------------------------------|

APOCYNACEAE

Apocynum androsaemifolium L.

HYDROPHYLLACEAE

Eriodictyon californicum (H. & A.) *Phacelia heterophylla* Pursh
Greene

BORAGINACEAE

Mertensia stomatechoides Kell.

LABIATAE

Agastache urticifolia (Benth.) Ktze. *Prunella vulgaris* L.
**Monardella odoratissima* Benth. *Pycnanthemum californicum* Torr.
**M. villosa* Benth. *Stachys albens* Gray

SCROPHULARIACEAE

Penstemon aggregatus Pennell *Penstemon Menziesii* Hook. ssp. *Davidsonii* (Greene) P. & K.
P. azureus Benth. *P. minor* (Gray) Keck
**P. Barrettae* Gray *P. nemorosus* (Dougl.) Trautv.
P. breviflorus Lindl. **P. Newberryi* Gray
P. Bridgesii Gray *P. ovatus* Dougl.
P. centranthifolius Benth. **P. pachyphyllus* Gray ex Rydb.
**P. confertus* Dougl. **P. procerus* Dougl. ex Grah.
P. euglaucus English **P. rupicola* (Piper) Howell
**P. fruticosus* (Pursh) Greene **P. saxosorum* Pennell
**P. glaber* Pursh **P. speciosus* Dougl.
**P. globosus* (Piper) P. & K. *P. strictus* Benth.
P. gracilentus Gray *P. subglaber* Rydb.
P. heterophyllus Lindl. *P. virens* Pennell
P. laetus Gray *P. Wilcoxii* Rydb.
P. Lemmonii Gray

CAPRIFOLIACEAE

Lonicera conjugialis Kell. *Symphoricarpus oreophilus* Gray
L. involucrata Banks *S. albus* (L.) Blake

COMPOSITAE

**Achillea borealis* Bong. **Artemisia ludoviciana* Nutt.
**A. lanulosa* Nutt. *A. pacifica* Nutt.
**A. millefolium* L. *A. pycnocephala* (Less.) DC.
Anaphalis margaritacea (L.) B. & H. **A. Rothrockii* Gray
Antennaria media Greene *A. saxicola* Rydb.
A. rosea Greene **A. Suksdorfii* Piper
Arnica foliosa Nutt. **A. vulgaris* L.
A. nevadensis Gray **Aster adscendens* Lindl.
**Artemisia Bolanderi* Gray *A. Andersonii* Gray
A. californica Less. *A. integrifolius* Nutt.
**A. Douglasiana* Bess. *Baccharis pilularis* DC.

Brickellia californica T. & G.	Haplopappus propinquus Blake
Chrysothamnus nauseosus (Pall.) Britt.	H. racemosus (Nutt.) Torr.
Erigeron Breweri Gray	H. squarrosus H. & A.
E. Coulteri Porter	H. venetus (HBK.) Blake
*E. salsuginosus Gray	H. Whitneyi Gray
Eriophyllum confertiflorum Gray	Helenium Bigelovii Gray
E. staechadifolium Lag.	H. Bolanderi Gray
E. lanatum (Pursh) Forbes	Helianthus californicus DC.
Grindelia camporum Greene	Senecio pauciflorus Pursh
G. cuneifolia Nutt.	S. Covillei Greene
Haplopappus apargioides Gray	*Solidago elongata Nutt.
H. carthamoides (Hook.) Gray	*S. multiradiata Ait.
H. Parryi Gray	Wyethia angustifolia Nutt.

INTERPRETATION OF DATA

In experimental work with biological materials, the treatment and interpretation of observed results is a matter of extreme importance. It is therefore essential to outline the general procedure used in arriving at the conclusions presented in the following chapters.

TAXONOMIC CONCLUSIONS. In certain plant groups, such as *Potentilla*, *Horkelia*, *Zauschneria*, *Achillea*, and *Artemisia*, a brief taxonomic discussion precedes the presentation of results from the varied-environment studies. The purpose of these systematic summaries is to orient the reader so that he will be better able to evaluate the experimental data that follow. They are based on all the evidence available, including morphological, geographical, and cytogenetic data, as well as evidence from the varied-environment experiments, and are intended to express our best present judgments concerning the relationships of the groups they treat. The experimental evidence on which these judgments are based is then presented in the pages following.

The principles used by the writers in arriving at taxonomic conclusions have been set forth elsewhere (Clausen, Keck, and Hiesey, 1939).

EVIDENCE FROM THE VARIED-ENVIRONMENT EXPERIMENTS. From the beginning, meticulous care has been exercised to insure the accuracy of all records. In view of the long-time nature of the investigations, dependable data are necessary to assure the identity of each plant and its attendant herbarium specimens and records. The value of the present evidence lies in the certainty of its validity.

Inasmuch as these experiments have covered many years, and especially since they furnish the principal part of the evidence on which conclusions of general biological importance rest, great care has been taken in interpreting the observed results. They have been studied and restudied from different points of view. The authors have discussed these data freely among themselves and with others who have seen the data and who have visited the transplant stations. Even after this careful analysis the writers realize that they have by no means exhausted all possibilities, but they are satisfied that the conclusions presented rest on matured judgment.

Biologists familiar with the variability of living materials will recognize at once the difficulties of interpreting such results as have accumulated during the past seventeen years from the varied-environment experiments. For example, there are gaps in our data as a result of difficulties inherent in the work. Plant losses by death, inability to propagate enough divisions from certain individuals, insect attacks, and problems of transportation were hindrances in the experiments. The necessity of moving plants from old to new gardens increased the casualties. Nevertheless, the body of accumulated evidence is large, and the results are ample to answer the questions that originally motivated these studies.

The evaluation of the significance of morphological differences that may be observed between two members of a clone growing in different conditions is a problem of great importance. Differences of opinion may arise in the minds of different investigators interpreting the same material. The critical reader will at once realize that many sets of variables are involved. These include, besides differences in the climatic complexes of different altitudes, the effect of different soils, local variations in environment, and annual fluctuations in weather conditions. To those trained in the rigorous discipline of plant physiology, these variables may appear hopelessly mixed.

While these shortcomings are readily granted, we wish to emphasize that the environmental conditions at any one of the three stations are fairly uniform. The plants are set far enough apart so that competition is practically excluded as a factor. The distance between plants is 1.5 m. at Stanford, 1 m. at Mather for most plants and 2 m. for the largest, and 1 m. at Timberline.

Soils are very uniform within the individual gardens. Experi-

ments on homozygous strains of tall, self-fertile annuals of *Madiinae* have shown that even highly modifiable characters like plant height vary but little from one plant to another, or from one section of the gardens to another, when the plants are so spaced that competition is excluded. Similarly, tests in the water-light gardens at Mather, where an effort was made to produce local environmental differences, indicate that even such unlike environments have very little effect on a character like earliness, whereas gross climatic differences between the stations and annual variations in climate have a spectacular effect.

Therefore, although the reactions recorded are responses to complexes of environmental factors, these are approximately the same for all plants in a plot at any given time. Also, the garden environment is not unlike the natural one under which some of the plants live. Although experiments like these can never replace laboratory tests under complete control, they offer an important supplement to them as an indicator of how the plants react under a series of natural conditions.

The three environmental complexes represented by the transplant stations produce a reaction, or modification, characteristic of each individual, namely a Stanford, a Mather, and a Timberline modification; these three form a reaction pattern of the individual. Related plants from the same or similar environments were discovered to have similar reactions, whereas plants from widely different environments may follow very different patterns. This makes it possible to arrange the plants in groups according to their reactions.

Therefore, to most ecologists, the present experiments represent a refinement of older methods. The writers have endeavored to discern the fundamentals that link the physiological and ecological viewpoints, and believe that the varied-environment investigations may serve to unify these now diverse fields by pointing out new experimental approaches, either quantitative or qualitative.

Much of the data has been subjected to statistical analysis, and the charts, graphs, and tables have for the most part been composed from the results of this mode of treatment. In spite of its powerful aid in many detailed analyses, it should be remembered that statistics, after all, is apt to become one-sided and cannot give a complete picture of living materials so complex as the transplants. In the final analysis, conclusions must largely rest on critical com-

parisons of individual plants rather than on groups of plants; therefore, close familiarity with the plants themselves in the different environments is necessary. The material illustrated has been selected with great care to represent what the writers consider to be typical examples. This is necessary because it is obviously impossible to present in this book more than a fraction of the evidence accumulated.

CYTOGENETIC DATA. Chromosome numbers are ordinarily a constant of the species and require no further interpretation so far as a given species is concerned. When relationships between species are considered, however, differences in chromosome number may indicate barriers that are of great significance. Also, their relation to the plant's environment and distribution and to morphological and physiological characteristics is of interest. Moreover, in polyploids, a study of chromosome numbers and chromosome behavior at meiosis sometimes gives substantial clues on phylogeny.

More important, however, are the results from actual breeding tests and hybridizations conducted in conjunction with cytological studies. To date it has been possible to investigate two groups of transplant perennials by this means, namely *Potentilla glandulosa* and *Zauschneria*. These studies have progressed the farthest in *Zauschneria*, and have led to a new comprehension of the organization of this genus, as summarized in chapter VI.

ACKNOWLEDGMENTS

In addition to their great debt to Dr. H. M. Hall, who initiated these investigations, the writers owe their thanks to others who have contributed to the work. Mr. John Coulter, of San Bruno, has recorded an appreciable amount of the observational data at the mountain stations in the Sierra Nevada during the summer seasons since 1931. Also, his care in handling the plants at these stations has contributed to the success of the experiments. During the year 1938-1939, Miss Suzanne Ravage assisted in the cytological technique and aided in counting the chromosomes of some of the forms. The graphs have been drawn by Mr. Richard Lucy, and part of the photographic work has been done by Mr. Berton Crandall, both of Palo Alto.

In the establishment and operation of the mountain stations, particularly Timberline, the Carnegie Institution has received generous cooperation from officials of the U. S. Forest Service.

II

POTENTILLA GLANDULOSA AND ITS ALLIES

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GENERAL RELATIONSHIPS

The group composed of *Potentilla glandulosa* and its allies has proved to be one of the most satisfactory in the transplant investigations, and, since the early realization of its possibilities by Dr. Hall, it has become the most important. Its wide vertical and horizontal distribution across temperate North America, combined with a great range of variability within its members, makes it well suited as a subject for attack on fundamental problems both of plant distribution in relation to environment and of plant relationship. The adaptability of its members both to garden manipulation and to changed environments makes them useful subjects for studies on environmental modification.

Potentilla glandulosa extends from the Pacific Coast to the Rocky Mountains, from British Columbia to northern Baja California, and from near sea level to alpine heights above 3000 m. In accordance with its ability to inhabit environments so different, it has developed a series of ecotypes fitted to various ecologic niches in this territory. In California, where most of the plants in the cultures originated, it is differentiated into four regional ecotypes in addition to two, at least, which are more local. The four major California ecotypes, of which three are illustrated in figure 8, are: (1) a Coast Range ecotype, ssp. *typica* (1077-4); (2) a Sierran foothill to mid-altitude ecotype, ssp. *reflexa*, occurring from 900 to about 2100 m. elevation (1093-14); (3) a subalpine ecotype in the Sierra Nevada from about 1500 to 2500 m. (see 1124-2 in fig. 26); and (4) an alpine ecotype, also in the Sierras, from about 2400 to 3500 m. (1113-6). The subalpine and alpine ecotypes both belong in ssp. *nevadensis*. These four ecotypes differ in many morphological

characteristics but especially in their seasonal rhythms and their reactions to different environments. They are but a sample of the diversity in this extremely variable species. The map locates them (fig. 13) and, also, those subspecies outside of California, many of



FIG. 8. Coastal, mid-Sierran, and alpine forms of *Potentilla glandulosa*.

Specimens of three individuals growing in a uniform garden at Mather, June 5-18, 1935: 1077-4, ssp. *typica*, dug December 22, 1922, near Montara, San Mateo County, California, near sea level; 1093-14, ssp. *reflexa*, dug July 9, 1926, at Mather, elevation 1400 m.; 1113-6, ssp. *nevadensis*, dug July 25, 1930, near Timberline station, elevation 3050 m.

which have not been cultivated but are recognized by their morphology alone.

There is no doubt that several of the subspecies of *Potentilla glandulosa* contain more than one ecotype, but they are morphologically alike, as are the two in ssp. *nevadensis*. For instance, it is almost certain that the high-montane forms of ssp. *typica*, from

the interior of Oregon and Washington and western Idaho, form a different ecotype from that in the Coast Ranges of California. The experimental evidence is too incomplete to be decisive on this point, but since the forms are morphologically alike and also doubtless closely connected in their evolutionary history, they are kept in one subspecies.

With its allies, *P. glandulosa* forms a very interesting complex of species that encircles almost the entire Northern Hemisphere, but



FIG. 9. *Potentilla arguta*, 1151-1, from Rock Creek, near Colorado Springs, Colorado, as it appeared when dug July 14, 1930, and five years later in the interstation garden at Mather.

none of the other species are nearly so variable as *glandulosa*. There are two additional North American species: *P. arguta* Pursh (fig. 9), which spans the continent at relatively low elevations from the Atlantic to the Pacific and from Nevada north to Yukon Territory, and *P. fissa* Nutt., a species distributed at high elevations in the Rocky Mountains (see map, fig. 12).



FIG. 10. *Potentilla rupestris* from Gärdsås, near Gothenburg, Sweden, as found in its native environment, and two-year-old seedlings grown at Stanford.

In the Old World there is one species with a distribution even wider than that of *P. arguta*, namely, *P. rupestris* L. (fig. 10). It extends from the Sea of Okhotsk across Asia to Asia Minor, the northern Mediterranean, central Europe, southern Sweden, and England. It is a species of lowlands and moderate elevations, rather uncommon and scattered, and not nearly as variable as *glandulosa*. In its native environment *P. rupestris* appears very similar to some forms of *glandulosa* or *arguta convallaria*, but when grown at Stanford it undergoes a strange modification and grows very poorly (see p. 99). The other Old World species of this complex are more local; one group of two centers in Asia Minor, the Caucasus, and Crimea (*P. geoides* M. B. and *P. calycina* Bois. & Bal.), another group of two in temperate Himalaya, and a fifth species in South Persia.

CYTOLOGY. This complex of species, so far as we know, has been able to encircle the world and to inhabit climates ranging from warm-temperate to arctic-alpine without change in chromosome number. Furthermore, the chromosomes are very few, for all forms investi-

gated are diploid, $n = 7$. These include *P. rupestris* (Tischler, 1929; Shimotomai, 1930; Popoff, 1935), *P. fissa*, *P. glandulosa* (three forms), and *P. calycina* (Shimotomai, 1930), *P. geoides*, and *P. arguta* (Popoff, 1935). This same number has been found in the forms used in the present experiments. Three plants of *P. arguta* and fifty-three plants of *P. glandulosa* were all diploid. The members of *P. glandulosa* counted (mainly by Miss Suzanne Ravage) include eleven plants of ssp. *typica*, two of ssp. *globosa*, three of ssp. *Hanseni*, fourteen of ssp. *reflexa*, and ten of the subalpine and eleven of the alpine ecotypes of ssp. *nevadensis*. These individuals came from widely distant points and are marked with a triangle in the survival diagrams (figs. 40-42). Three plants not represented in these diagrams were also counted, namely, the montane form of ssp. *typica*, from 2000 m. altitude in the Wallowa Mountains, northeastern Oregon (1148-1); ssp. *arizonica*, from 2750 m. altitude at Puffer Lake, Beaver County, Utah (1149-1); and a plant of *P. rupestris*. These also had $n = 7$. The chromosomes are small, in the somatic stage one to two microns long, and in the meiotic one micron in diameter.

GENETIC EVIDENCE. Experimental evidence proves that there are no genetic barriers separating the geographically and morphologically most distinct forms of *P. glandulosa* in California. Considering the constancy in chromosome number and the morphologic intermediates in nature, where *P. arguta*, *fissa*, and *glandulosa* meet and overlap, it appears also certain that these three are no more distinct than ecospecies that are members of one cenospecies (Clausen, Keck, and Hiesey, 1939). Experimental evidence might even eventually demonstrate that all are members of one huge ecospecies.

Fragmentary experimental evidence published on the Eurasiatic species of this group (Popoff, 1935) indicates that *P. rupestris* and the Crimean-Caucasian *P. geoides* are genetically very closely related; it is even possible that they are ecotypes of one ecospecies. *Potentilla geoides* is a taxonomic unit morphologically very similar to some forms of *P. glandulosa* (Wolf, 1908). Unfortunately, Popoff did not sow the seeds he obtained in the cross *P. arguta* \times *P. geoides*. This hybrid offspring would have determined whether or not the two are able to exchange genes. Crossings between *P. arguta* and *P. rupestris* were unsuccessful in both directions, which shows that

these two are distinct species. It is probable that the New World and the Old World species of this complex will finally prove to belong to one cenospecies, which then would be called *Potentilla rupestris*, after the first-named member of the complex. Until this has been demonstrated, however, we shall consider them as two cenospecies, using *Potentilla arguta* as the collective name to be applied to the North American complex.

PROBABLE ORIGINS. Both the Eurasiatic and the American species appear to have had a common evolutionary origin. Morphologically they stand out among the *Potentillas*, and the interspecific differences are not impressive when the intraspecific variation is considered. The characters that distinguish members of the American group from one another recombine in almost all possible ways in the present-day taxonomic units, as shown in table 1 (p. 36). This suggests that they represent rather simple genic recombinations.

The greatest variation centers around the Columbia River basin in northwestern North America, and the unit that appears to be morphologically the most central is *P. arguta* ssp. *convallaria*. It connects directly with much of the variation in North America and is morphologically the closest approach on this continent to the Eurasian *P. rupestris*. It is therefore possible that the evolutionary center from which this whole complex has spread is around the Columbia River basin. Following general migration routes from here, the members could spread to the northwest, south, and east as geologic revolutions took place that opened new environments to be occupied by races fitted to them through nature's constant experimentation in crossing, segregation, and selection.

In order to give a coordinated picture of the available facts, this chapter will present: (1) the formal taxonomic treatment of the American complex, cenospecies *P. arguta*; (2) the effect of varied environment on uniform heredity and of uniform environment on varied heredity; and (3) the results of recombining the heredity by crossing the plants.

TAXONOMY

In order to interpret the transplant data on any group, it is first necessary to understand the natural units. But if we are to improve upon existing taxonomic treatments, it is likewise necessary to

weigh the experimental data obtained from transplanting, cytology, and crossing tests.

As indicated above, the complexity of *Potentilla glandulosa* and its allies is due to the great diversity of form, in part correlated with the wide variety of environments occupied, and to an apparent absence or weakness of genetic barriers. The following taxonomic synopsis is based as far as possible on our experimental results, and on inspection of all the herbarium material in the United States National Herbarium, New York Botanical Garden, Academy of Natural Sciences of Philadelphia, Rocky Mountain Herbarium of the University of Wyoming, University of California, Dudley Herbarium of Stanford University, California Academy of Sciences, and the Carnegie Institution. E. L. Greene's types were examined at the University of Notre Dame. The specimens in these herbaria have been annotated.

In the most recent treatment of the group, Rydberg (1908) assigned *Potentilla glandulosa* to the genus *Drymocallis* and maintained twenty-eight species in North America. All of these now appear to be members of three taxonomic species, *P. arguta* Pursh, *P. fissa* Nutt., and *P. glandulosa* Lindl., which are possibly three ecospecies of one cenospecies.

We are able to recognize eleven distinct subspecies in *P. glandulosa*, but the experiments indicate that there are even more ecotypes. That all this diversity should be included in one taxonomic species is shown by the experimental results, but the morphological evidence alone points to much recombination, for almost all the subspecies link in one or more directions through intermediates and hybrids. A study of the distribution map (fig. 13) shows how many opportunities are offered in nature for the members of this species to meet.

In our opinion there is no justification for excluding *Drymocallis* from *Potentilla*. Certain species undoubtedly belonging to *Potentilla* closely link *Drymocallis* to the main body of the genus. We do believe, however, that the morphological distinctions of the anther and the position of the style, combined with a homogeneity of form, justify the maintenance of *Drymocallis* as a section or subsection of *Potentilla*.

The ecotypes within *Potentilla glandulosa* have been worked out experimentally in the same manner that has been followed with other perennial plants, namely, by determining the number of groups

within the species that differ from one another ecologically and physiologically. In the majority of cases these also differ morphologically. Characters that have proved important in making these determinations include geographical distribution, morphology, and reactions to transplanting, including vigor, time of flowering, ability to ripen seed, and ability to survive. These points are considered in detail below, but it should be emphasized that we have found it important to consider them all. The ecotypes have been the basis for our taxonomic treatment, for we consider a morphologically distinguishable ecotype the equivalent of a subspecies. As shown in the treatment of *P. glandulosa*, the ecotype (a genetic-ecologic unit) may not always coincide with the subspecies (a systematic unit). This is because ecotypes are not always morphologically distinct, and they must then be retained within one systematic unit or subspecies.

KEY TO THE NORTH AMERICAN MEMBERS OF POTENTILLA,
SECTION DRYMOCALLIS

- A. Leaflets 9-11, decreasing appreciably and regularly in size from apex of leaf to the short petiolar portion (blade wedge-shaped in outline), deeply incised, rudimentary leaflets often interspersed; stems stout, 1.5-3 dm. tall, arising from long slender stolons; flowers aggregated, large, white.....1. *P. fissa*
- AA. Leaflets 5-9 and decreasing inappreciably and irregularly in size to the relatively long petiolar portion (except in 3*k*), rudimentary leaflets absent or, if present, at base of blade.
 - B. Cyme short, dense; stem stout, 3-10 dm. tall, densely viscid-villous; stolons usually absent; petals white, 6-8 mm. long.....2. *P. arguta*
 - C. Stems very stout, anthocyanous, prominently brown-villous; cyme essentially capitate; sepals to 15 mm. long. Principally east of the Continental Divide.....2*a*. *P. a.* ssp. *typica*
 - CC. Stems less stout, less anthocyanous and villous; cyme merely condensed; sepals to 12 mm. long. Principally west of the Continental Divide...2*b*. *P. a.* ssp. *convallaria*
- BB. Cyme open or, if condensed, stem not stout or densely viscid-villous and the flowers smaller; petals usually cream or yellow, sometimes nearly white.....3. *P. glandulosa*
- D. Petals much longer than the sepals. Plants of mid- and high altitudes (cf. 3*c*).

- E. Petals canary yellow; inflorescence leafy-bracted, the bracts rhombic, the branches divergent.....3a. *P. g.* ssp. *glabrata*
- EE. Petals creamy white; inflorescence not leafy-bracted, the branches erect.
- F. Leaflets \pm densely beset with stalked glands, small. Principally Rocky Mountain3d. *P. g.* ssp. *pseudorupestris*
- FF. Leaflets pilose but not glandular, usually larger. Pacific Coast states.
- G. Herbage glabrate (sometimes moderately pilose); cyme open; stolons elongated; akenes *ca.* 0.8 mm. long3e. *P. g.* ssp. *nevadensis*
- GG. Herbage strongly hirsute; cyme congested; stolons very short; akenes *ca.* 1 mm. long3f. *P. g.* ssp. *ashlandica*
- DD. Petals slightly if at all longer than the sepals. Plants of low or moderate elevations, except 3b and 3c.
- H. Leaflets average mostly more than 15 mm. long, principally on anterior half of rachis; stems mostly much more than 10 cm. tall; sepals 7 mm. or more long (except in 3j).
- I. Petals equaling or slightly exceeding the sepals, broad.
- J. Branches erect, not leafy above, scarcely anthocyanous or glandular; sepals broadly lanceolate, to 10 mm. long.
- K. Inflorescence congested; stems 1.5–4.5 dm. tall; petals spreading; akenes not beaked. Utah-Arizona3c. *P. g.* ssp. *arizonica*
- KK. Inflorescence open; stems 4–8 dm. tall; petals erect; akenes subrostrate. Mid-altitude in the Sierra Nevada, rare.....3g. *P. g.* ssp. *Hansenii*
- JJ. Branches divaricate, leafy-bracted above, anthocyanous, prominently glandular; sepals ovate, to 12 mm. long.....3i. *P. g.* ssp. *typica*

- II. Petals shorter than the sepals, narrow.
 - L. Petals cream white, erect or ascending at anthesis; branching erect; cyme condensed.
 - M. Sepals to 6 mm. long; petals erect, the flower at anthesis globose; stems 2-4 dm. tall, velvety, green or anthocyanous. Oregon-California3j. *P. g. ssp. globosa*
 - MM. Sepals to 10 mm. long; petals ascending, the flower at anthesis broadly campanulate; stems 4-6 dm. tall, moderately villous, not anthocyanous. Rocky Mountains3b. *P. g. ssp. micropetala*
 - LL. Petals deep yellow, reflexed or spreading at anthesis; branching divaricate; cyme open; stems anthocyanous. California3h. *P. g. ssp. reflexa*
 - HH. Leaflets up to 6 mm. long, up to 12 in number, extending most of the length of the rachis; herbage \pm silky pubescent; stems only 8-12 cm. tall, from slender stolons; sepals 5 mm. long3k. *P. g. ssp. Ewarii*

Because dichotomous keys cannot give all the points of difference between any two entities in a rather extended series, it is well to have supplementary descriptions of the units. In this case we have tabulated the principal variables in this complex as they occur in each unit, so that either the characters themselves or the units may be compared directly (table 1).

DIFFERENCES IN AKENES. Differences in size, color, and venation of the akenes have never been stressed in accounts of the species of the section *Drymocallis*, but in the present studies they have been found of some use. The graph in figure 11 shows the variation in and the relative differences between most of the California subspecies of *P. glandulosa* as regards akene length; ssp. *typica* has the largest akenes, and the alpine ecotype of ssp. *nevadensis* has the smallest. The akenes of sspp. *typica* and *reflexa* are dark brown and venulose, while those of the other two subspecies are pale brown or buff and more faintly venulose.

TABLE 1
ANALYSIS OF CHARACTERS IN THE GENOSPECIES *POTENTILLA ARGUTA*

UNIT	PETALS		INFLORESCENCE			SEALS, MAXIMUM SIZE (mm.)	GLANDS	STEM		STOLONS	SEEDS		LEAFLETS, SIZE AND NUMBER
	Size	Direction	Color	Branching	Density	Leafy- bracted		Pubescence	Antho- cyanin		Size	Beak	Color
1. <i>Potentilla frisa</i>	large	spreading	cream	erect, short	congested (cymose)	+	10	many	shaggy (brownish)	±	low	many (long)	medium brown
2a. <i>P. arguta</i> ssp. <i>typica</i>	large	spreading	white	erect, short	congested (capitate)	+	15	abundant	shaggy (brownish)	+	(-)	tall	medium brown
2b. <i>P. arguta</i> ssp. <i>convallaria</i>	large	spreading	white	erect, short	congested (approximate)	+	12	abundant	shaggy (brownish)	+	(-)	tall	medium brown
3a. <i>P. glandulosa</i> ssp. <i>glabrata</i>	large	spreading	canary yellow	divergent, elongated	open	+	12	rather few	villous	-	tall	few (short)	medium, brown
3b. <i>P. glandulosa</i> ssp. <i>micropetala</i>	small	ascending	cream	divergent, elongated	±open	+	10	rather few	±villous	-	tall	few (short)	medium, brown
3c. <i>P. glandulosa</i> ssp. <i>arizonica</i>	medium	spreading	cream white	erect, short	congested (±capitate)	-	10	rather few	±villous	-	low	few (short)	medium, brown
3d. <i>P. glandulosa</i> ssp. <i>pseudorupestris</i>	large	spreading	cream	erect, ±short	±open	-	10	abundant (many)	glutinous- villous	-	(+)	low	small, (5-7)(-9)
3e. <i>P. glandulosa</i> ssp. <i>nevadensis</i>	large	spreading	cream white	erect, elongated	±open	-	10	almost none	glabrate (±pilose)	-	low (tall)	many (long)	medium, brown
3f. <i>P. glandulosa</i> ssp. <i>asilandica</i>	large	spreading	cream white	erect, ±short	congested (approximate)	-	10	few	very hirsute	-	(+)	medium	medium, brown
3g. <i>P. glandulosa</i> ssp. <i>Hansenii</i>	medium	±erect	cream	erect, elongated	±open	-	10	few	vilose	-	tall	several	medium, brown
3h. <i>P. glandulosa</i> ssp. <i>reflexa</i>	small	reflexed	deep yellow	divaricate, elongated	open	-	10	many	±densely vilose	+	tall	few (short)	large, red- brown
3i. <i>P. glandulosa</i> ssp. <i>typica</i>	medium	ascending- erect	cream white	divaricate, elongated	open	+	12	abundant	densely villous	+	medium	few or none	large, dark brown
3j. <i>P. glandulosa</i> ssp. <i>globosa</i>	small	erect	white	erect, short	congested (cymose)	+	6	almost none	velutinous	±	low	few (short)	medium, brown
3k. <i>P. glandulosa</i> ssp. <i>Ewanii</i>	small	erect	?	divergent, ±short	open	-	5	rather few	appressed- hirsute	±	very low	many (long)	very small, (7-11)

1. *POTENTILLA FISSA* Nutt. in Torr. & Gray, Fl. N. Amer. 1:446, 1840

Potentilla scopulorum Greene, Erythea 1:4, 1893. Type locality, Upper Bear Creek, Colorado, *Greene*. Type verified at Notre Dame.

Drymocallis fissa Rydb., Mem. Dept. Bot. Columbia Univ. 2:197, 1898.

Potentilla glandulosa var. *fissa* Wolf, Bibl. Bot. 16(71):136, 1908.

A species principally of high montane distribution, from the Black Hills of South Dakota and the Big Horn Mountains of Wyoming,

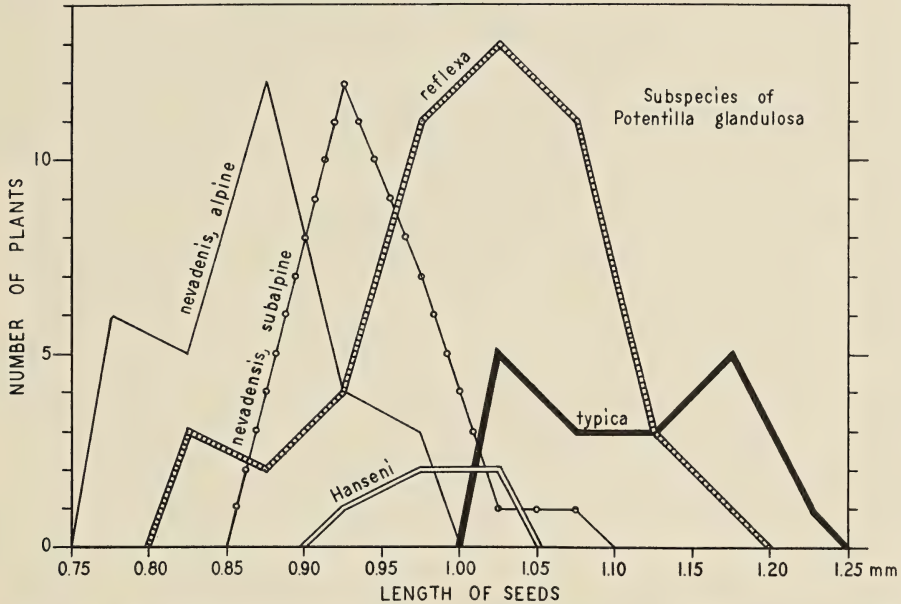


FIG. 11. Frequency distribution curves of akene lengths of five ecotypes of *Potentilla glandulosa*.

Each individual was classified on the basis of the mean length of ten akenes picked at random. All plants were growing in a uniform garden at Mather, and the akene samples were taken in 1937. The alpine ecotypes have the smallest akenes, the lowland the largest.

southward through the Rocky Mountains to northern New Mexico (fig. 12). Type locality, southern Wyoming, *Nuttall*. Type verified at Academy of Natural Sciences, Philadelphia.

Intermediates occur between this species and the following, but for the most part *P. fissa* is quite distinct.

2. *POTENTILLA ARGUTA* Pursh, Fl. Amer. Sept. 2:736, 1814

2a. *Potentilla arguta* Pursh ssp. *typica* Keck nom. nov.

Potentilla arguta Pursh, loc. cit.

Drymocallis agrimonioides (Pursh) Rydb., N. Amer. Fl. 22:368, 1908.

(Detailed synonymy in N. Amer. Fl. 22:368, 1908.)

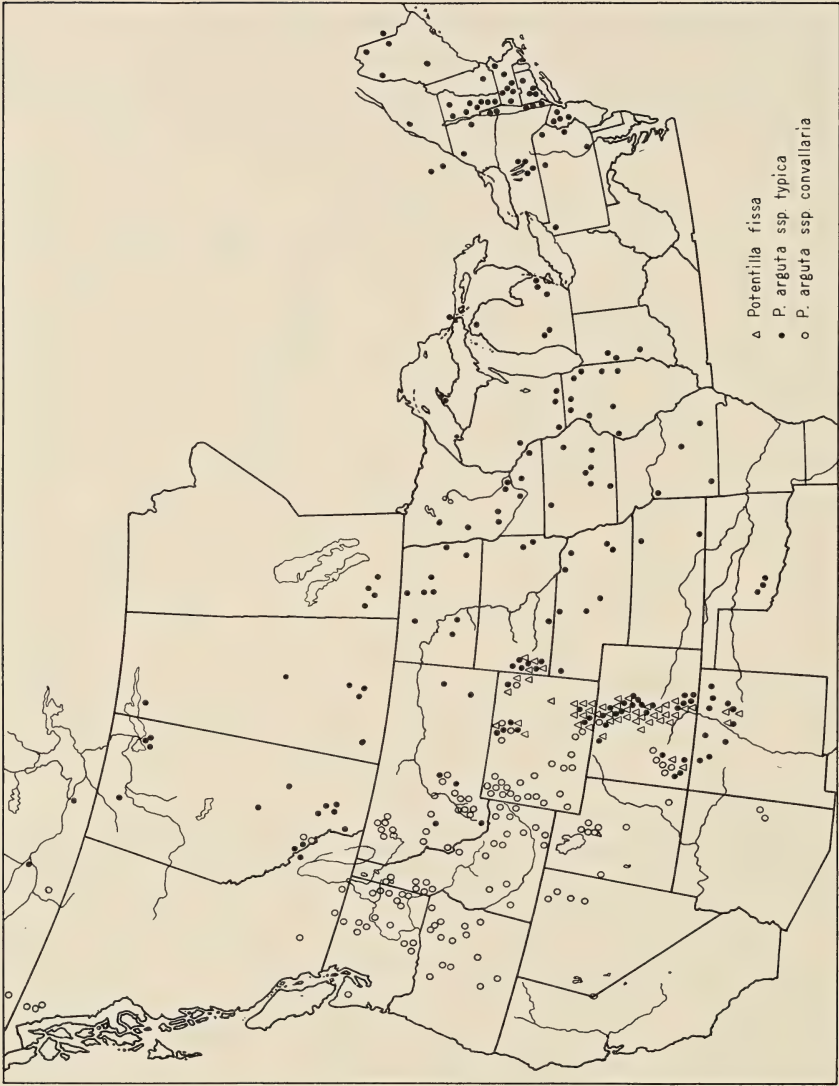


FIG. 12. Distribution of *Potentilla fissa* and *P. arguta* as determined from collections in various herbaria.

New Brunswick to New Jersey, westward to Oklahoma and Colorado, northward to Mackenzie (Slave Lake and Fort Simpson) (fig. 12). Type locality, "in Upper Louisiana, *Bradbury*." Type verified at Philadelphia.

This species is relatively constant over its extensive range, although the size of the plant and the amount of the pubescence are variables. Specimens distinctly within the range of this geographical unit (North Dakota, for example) may be about as glabrate as those of the following subspecies. Intermediates are frequently found in the region of the Continental Divide.

2b. *Potentilla arguta* Pursh ssp. *convallaria* (Rydb.) Keck comb. nov.

Potentilla convallaria Rydb., Bull. Torr. Club 24:249, 1897.

Drymocallis convallaria Rydb., Mem. Dept. Bot. Columbia Univ. 2:193, 1898.

Potentilla arguta var. *convallaria* Wolf, Bibl. Bot. 16(71):134, 1908.

Drymocallis corymbosa Rydb., N. Amer. Fl. 22(4):369, 1908. Type, from Spanish Basin, Montana, *Rydberg & Bessey 4348*, verified at New York.

Yukon Territory (White Horse) and northern British Columbia (Lake Atlin), southward through the Rocky Mountains to Wyoming, northern and western Colorado, Arizona (White Mountains), and northeastern Nevada; westward to the base of the Cascade Range in Washington and Oregon; local, also, on the Olympic Mountains (fig. 12). The type, from near Bozeman, Montana, *Flodman 604*, verified at New York.

Because it is located in the midst of other units with which it is evidently able to cross to some extent, ssp. *convallaria* shows considerable variability in almost all its characters. As a whole, it seems to be linked with *P. arguta* rather than with *P. glandulosa*.

Potentilla glutinosa Nutt. ap. Rydb., Bull. Torr. Club 23:245, 1896, as typified by Nuttall's specimen at Philadelphia, and an isotype sheet at New York, is unidentifiable. In fact, it appears likely that parts of two different units may have been mixed, one of which is probably referable to *P. fissa*, while the other may be *P. arguta convallaria*. These fragmentary specimens make the unit entirely uncertain.

3. POTENTILLA GLANDULOSA Lindl., Bot. Reg. 19:pl. 1583, 1833

Figures 8 and 13

3a. *Potentilla glandulosa* ssp. *glabrata* (Rydb.) Keck comb. nov.

Drymocallis glabrata Rydb., Mem. Dept. Bot. Columbia Univ. 2:200, 1898.

Potentilla glandulosa var. *glutinosa* f. *glabrata* Wolf, Bibl. Bot. 16(71):137, 1908.

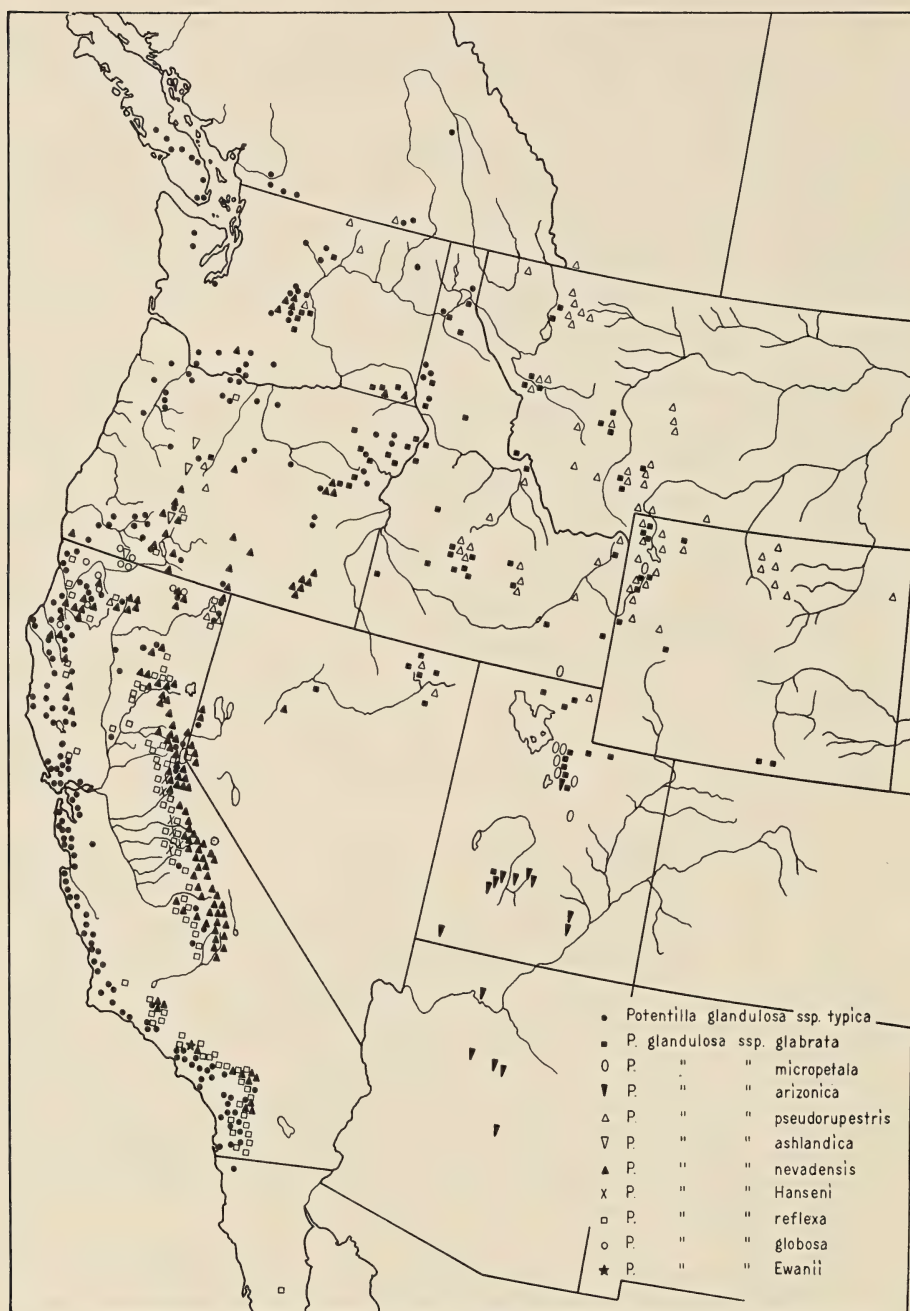


FIG. 13. Distribution of the subspecies of *P. glandulosa* as determined from collections in various herbaria.

Drymocallis foliosa Rydb., N. Amer. Fl. 22(4):371, 1908. Type, from Bridger Mountains, Montana, *Flodman 596*, verified at New York.

Northern Montana to western Wyoming, central Utah and Nevada, westward to Washington and Oregon. The type, from eight miles southwest of Ellensburg, Washington, *Elmer 412*, seen at New York.

This unit, like *P. arguta convallaria*, is morphologically and geographically connected with several others. There are evident transitions from this to ssp. *arizonica*, *micropetala*, *pseudorupestris*, *nevadensis*, and *P. arguta convallaria*.

3b. *Potentilla glandulosa* ssp. *micropetala* (Rydb.) Keck comb. nov.

Drymocallis micropetala Rydb., N. Amer. Fl. 22(4):375, 1908.

This form occurs at elevations of 1500 to 2900 m. in the Wasatch Mountains of Utah, and possibly in adjacent Idaho; also in Yellowstone Park, but perhaps only in atypical form. The type, from City Creek Canyon, Salt Lake County, Utah, *Rydberg 6153*, seen at New York.

3c. *Potentilla glandulosa* ssp. *arizonica* (Rydb.) Keck comb. nov.

Drymocallis arizonica Rydb., N. Amer. Fl. 22(4):373, 1908.

Potentilla MacDougalii Tidestrom, Proc. Biol. Soc. Wash. 48:39, 1935. New name for *Drymocallis arizonica* Rydb.

Potentilla arizonica Rydb. in Tidestrom, *ibid.*, as synonym. Not *P. arizonica* Greene, 1887.

In the mountains of central and southern Utah, at elevations of 2400 to 3500 m., but descending below 2000 m. in northern Arizona; extending from above Provo, Utah, to the Matzatzal Mountains, Arizona. The type, from Mormon Lake, Coconino County, Arizona, *MacDougal 64*, seen at New York.

3d. *Potentilla glandulosa* ssp. *pseudorupestris* (Rydb.) Keck comb. nov.

Potentilla pseudorupestris Rydb., Bull. Torr. Club 24:250, 1897.

Drymocallis pseudorupestris Rydb., Mem. Dept. Bot. Columbia Univ. 2:194, 1898.

Drymocallis pseudorupestris var. *intermedia* Rydb., Mem. N. Y. Bot. Gard. 1:220, 1900, in part.

Potentilla rupestris var. *americana* Wolf, Bibl. Bot. 16(71):129, 1908. Chiefly founded on *P. pseudorupestris* Rydb.

Drymocallis viscosa Rydb., N. Amer. Fl. 22:372, 1908. Type, from meadows on Mount Chapaca, Washington, *A. D. E. Elmer 564*, seen at New York.

Southern Alberta and British Columbia, through western Montana and Wyoming to northernmost Utah and Nevada, to Idaho; less frequent in Washington and on the Cascades of Oregon, to Mount Eddy, California; usually at high elevations. The type, from Long Baldy, Little Belt Mountains, Montana, *Flodman 598*, seen at New York.

This subspecies becomes most robust and glandular in Missoula County, Montana. In Idaho and adjacent Nevada it is often very little glandular and the leaves may be quite smooth; yet it is readily distinguishable from ssp. *nevadensis*, in which the leaves are definitely pubescent but not glandular.

3e. *Potentilla glandulosa* ssp. *nevadensis* (S. Wats.) Keck comb. nov.

Potentilla glandulosa var. *nevadensis* S. Wats., Bot. Calif. 1:178, 1876.

Potentilla glandulosa var. *lactea* Greene, Fl. Franciscana 65, 1891. The original description was taken from a water-color painting, as Greene confided to Rydberg in a letter. From the Sierra Nevada, California.

Potentilla lactea Greene, Pittonia 3:20, 1896.

Drymocallis glandulosa var. *monticola* Rydb., Mem. Dept. Bot. Columbia Univ. 2:199, 1898. New name for *P. glandulosa* var. *nevadensis* S. Wats.

Drymocallis cuneifolia Rydb., *ibid.* 204. Described from a specimen in early flower from the San Bernardino Mountains, California, *Parish 1818*. Type verified at New York. The slender, elongated styles do not prove to distinguish a natural subgroup here; in the type specimen they are immature.

Drymocallis gracilis Rydb., Bull. Torr. Club 28:177, 1901. A form from Pine Ridge, Fresno County, California, *Hall & Chandler 138*. Type verified at New York. This is the subalpine ecotype, here included with an alpine ecotype in this subspecies because the two are morphologically indistinguishable, as discussed under the transplant results. The plant 1124-2, figure 25, is from this locality.

Potentilla rupestris var. *americana* Wolf, Bibl. Bot. 16(71):129, 1908, in part.

Potentilla glandulosa var. *genuina* f. *monticola* Wolf, *ibid.* 136.

Potentilla cuneifolia Wolf, *ibid.* 139. Not *P. cuneifolia* Bertol., 1863.

Potentilla monticola Fedde, Just Bot. Jahresb. 36(2):494, 1908.

Potentilla pumila Fedde, *ibid.*

Drymocallis lactea Rydb., N. Amer. Fl. 22(4):369, 1908.

Drymocallis monticola Rydb., *ibid.* 370.

Drymocallis pumila Rydb., *ibid.* 372. The alpine ecotype from Steins Mountains, Oregon, *Cusick 2571*. Type verified at New York.

Potentilla glandulosa var. *monticola* Jeps., Man. Fl. Pl. Calif. 487, 1925.

Potentilla Peirsonii Munz, Bull. So. Calif. Acad. 31:65, 1932. New name for *P. cuneifolia* Wolf.

Potentilla glandulosa var. *Austinae* Jeps., Fl. Calif. 2:181, 1936. The type, from Quincy, Plumas County, California, *Heller 10863*, verified at University of California, is probably a hybrid between ssp. *nevadensis* and ssp. *reflexa*. Of the remaining four collections cited, one is referable to ssp. *reflexa*, the others to ssp. *nevadensis*.

Potentilla glandulosa var. *Peirsonii* Jeps., *ibid.*

From the Cascade and Blue Mountains of Washington, southward through Oregon to the North Coast Range, Sierra Nevada, and San Bernardino and San Jacinto Mountains of California, at elevations of 1500 up to 3500 m., in meadows and on moist rocky slopes. Type locality, South Fork of Kern River, California, *Rothrock*. Type verified at Gray Herbarium.

This unit intergrades with sspp. *pseudorupestris*, *reflexa*, *Hansenii*, and *ashlandica*. It consists of two ecotypes: one is a dwarf, early-flowering alpine that occurs above 2600 m., while the other is sub-alpine and may be distinguished in garden cultures by its taller stature and later flowering. Since the differences between the two are not sufficiently distinct to be recognized in the field or in the herbarium with certainty, the two ecotypes are here included in one subspecies.

3f. *Potentilla glandulosa* ssp. *ashlandica* (Greene) Keck comb. nov.

Potentilla ciliata Howell, Fl. N. W. Amer. 1:175, 1898. Not *P. ciliata* Greene, 1887.

Potentilla ashlandica Greene, Pittonia 3:248, 1898. New name for *P. ciliata* Howell.

Drymocallis ashlandica Rydb., Mem. Dept. Bot. Columbia Univ. 2:200, 1898.

Potentilla glandulosa var. *fissa* f. *ashlandica* Wolf, Bibl. Bot. 16(71):137, 1908.

Oregon, in the Cascade Mountains, from Linn County southward to the Siskiyou Mountains, Jackson County, at elevations of 1500 to 2000 m.; uncommon. Type locality, Siskiyou Mountains, near Ashland Butte, July 8, 1897, *T. Howell*. Probable isotype and phototype verified.

3g. *Potentilla glandulosa* ssp. *Hansenii* (Greene) Keck comb. nov.

Potentilla Hansenii Greene, Pittonia 3:20, 1896.

Drymocallis Hansenii Rydb., Mem. Dept. Bot. Columbia Univ. 2:200, 1898.

Potentilla glandulosa var. *genuina* f. *Hansenii* Wolf, Bibl. Bot. 16(71):136, 1908.

California, on the west flank of the Sierra Nevada, occasional from Amador County to Mariposa County, in meadows at eleva-

tions of 1200 to 1800 m. The type, from moist ground toward the Stanislaus River, south of Calaveras Big Trees, taken in 1889 by E. L. Greene, verified at Notre Dame.

This subspecies is evidently a recombination form that has become stabilized, combining features of ssp. *nevadensis* and *reflexa*.

3h. *Potentilla glandulosa* ssp. *reflexa* (Greene) Keck comb. nov.

Potentilla glandulosa var. *reflexa* Greene, Fl. Franciscana 65, 1891.

Potentilla reflexa Greene, Pittonia 3:19, 1896.

Drymocallis reflexa Rydb., Mem. Dept. Bot. Columbia Univ. 2:203, 1898.

Drymocallis viscida Parish, Bot. Gaz. 38:460, 1904. The usual form; type from Snow Canyon, Mill Creek, San Bernardino Mountains, California, Parish 5060. Type verified at Dudley Herbarium.

Potentilla laxiflora Fedde, Just Bot. Jahresb. 36(2):494, 1908.

Drymocallis laxiflora Rydb., N. Amer. Fl. 22(4):374, 1908. The usual form; type from Big Tree Canyon on the road from Three Rivers to Mineral King, Tulare County, California, Coville & Funston 1355. Type verified at United States National Herbarium.

Cascade Mountains, Oregon (rare), southward through California (common), in the North Coast Range, Sierra Nevada, mountains of southern California, to Sierra San Pedro Martir, Baja California. Type locality, dry ground not far from Calaveras Big Trees, June 1889, Greene. Type verified at Notre Dame.

This subspecies corresponds to the foothill ecotype and inhabits the dry and warm foothill regions, but on hot westerly slopes it may ascend as high as 2200 m. It crosses the Sierra Nevada through Donner Pass and is fairly frequent about Lake Tahoe. All along the Sierra Nevada at the upper limits of its range, *reflexa* meets and hybridizes with ssp. *nevadensis*, usually with the subalpine ecotype.

3i. *Potentilla glandulosa* ssp. *typica* Keck nom. nov.

Potentilla glandulosa Lindl., Bot. Reg. 19:pl. 1583, 1833.

Potentilla Wrangelliana Fisch. & Avé-Lall., Ind. Sem. Hort. Petrop. 7:54, 1840.

Type locality, Russian Settlement, California (Fort Ross). The coarse, maritime form. The supposed differences in flower color and sepal shape, that have been used to distinguish this from *glandulosa*, do not mark off a distinct morphological unit and much less an ecological unit.

Potentilla arguta var. *glandulosa* Cockerell, W. Amer. Sci. 5:11, 1888.

Potentilla valida Greene, Pittonia 3:20, May 1, 1896. The type, seen in the Greene Herbarium at Notre Dame, from Victoria, Vancouver Island, is a fruiting specimen of typical *P. glandulosa*. One evidence of this is its

large akenes. With this specimen, Greene put other collections with much smaller akenes that are representative of ssp. *glabrata* of the interior. Both Greene and Rydberg proceeded to interpret *valida* as the material now known as ssp. *glabrata*.

Potentilla rhomboidea Rydb., Bull. Torr. Club 23:248, June 1896. From Deer Creek Mountains, southwestern Oregon, July 5, 1887, *Howell*. Type verified at New York. A montane form of this subspecies. Rydberg emphasized the slender styles in proposing this entity, but the character does not prove to have value in this group. There is considerable variation in the thickness of the style, but apparently not in connection with other morphological characters of importance or geographical distribution.

Drymocallis glandulosa Rydb., Mem. Dept. Bot. Columbia Univ. 2:198, 1898.

Drymocallis Wrangelliana Rydb., *ibid.* 201.

Drymocallis rhomboidea Rydb., *ibid.* 203.

Potentilla glandulosa var. *genuina* Wolf, Bibl. Bot. 16(71):136, 1908.

Potentilla glandulosa var. *Wrangelliana* Wolf, *ibid.* 137.

Drymocallis amplifolia Rydb., N. Amer. Fl. 22:373, 1908. From near the Columbia River, western Klickitat County, Washington, *Suksdorf 1761*. Type verified at New York. A shade form, otherwise perhaps the same race as *D. albida*.

Drymocallis oregana Rydb., *ibid.* 374. The name taken from Nuttall, originally published in synonymy by Torrey & Gray, Fl. N. Amer. 1:446, 1840. The type in the Torrey Herbarium is labeled in Nuttall's hand, "Columbia R. a gigantic specimen." There is an isotype in Philadelphia. The large specimens are very glandular-pubescent, small-petaled, and in early flower. The inflorescence is branched but not very open. However, there seem to be only side branches preserved.

Drymocallis albida Rydb., *ibid.* 375. From damp or shady places at Bingen, Klickitat County, Washington, *Suksdorf 2209*. Type seen at New York. Not obviously a shade form as is *D. amplifolia*.

Southern British Columbia and Vancouver Island, southward to northern Baja California; most abundant near the coast at low elevations, but occurring in a morphologically indistinguishable form in the mountains from eastern British Columbia to northeastern California, and in adjacent Idaho, ascending to about 2400 m. Also occasional in the foothills of the Sierra Nevada. The type was collected by Douglas in California, probably near Monterey. A photo-type has been studied.

We find this subspecies to be quite susceptible to modification, as will be seen in detail later. Plants that appear very different in the wild, as for example one from the open coast as compared with one from a forested inland hillside, become remarkably similar when grown side by side in the garden. The types of *P. glandulosa* and

P. Wrangelliana perhaps came from environments similarly diverse. The sepals in this subspecies are remarkably accrescent and differ in appearance depending upon their stage of development. Petal color does not vary greatly; in living material it is white or creamy white, slightly yellow toward the base. In drying, the petals sometimes appear whitish, sometimes yellow.

We recognize that this subspecies is heterogeneous. The forms from the vicinity of the California coast are the most coarse in texture, but they intergrade by imperceptible steps into more slender forms in southern Oregon and elsewhere. In the interior, from Washington to northern California, ssp. *typica* often ascends to elevations of 2000 to 2400 m., but without sufficient morphological change to make it distinguishable from the forms that occur nearer to the coast. It differs in its physiological reactions, however, for it flowers about two weeks later at Stanford than do the Coast Range materials, although at Mather all forms flower at the same time. In this respect it is similar to another montane form of restricted distribution in the southern Sierra Nevada discussed further below.

The material of this subspecies from the coastal region of southern Oregon and California constitutes a Coast Range ecotype.

3j. *Potentilla glandulosa* ssp. *globosa* Keck ssp. nov.

Caulibus 2–4 dm. altis erectis robustis foliosis, supra ramis erectis cymoso-compactis plurifloris, foliis dense villosis vel canescentibus vix glandulosis, sepalis moderate magnis erectis, petalis incurvis calycem paulo brevioribus vel aequalibus albidis, acheniis relative magnis ovoideis brunneis. Type: *Keck 4841* (Herbarium of the University of California), from east side of Mount Ashland, Jackson County, Oregon, at 1950 m. elevation, in chaparral and open forest, August 7, 1938; in fruit. Isotype Carnegie Institution.

Frequent in the Siskiyou and Salmon Mountains, from Mount Ashland, Oregon, to South Fork Mountain, Humboldt County, California, at elevations of 1280 to 2150 m., and in the Lava Beds National Monument.

OREGON. Jackson Co.: Mount Ashland, *Kildale 8077* (Stanford), *Keck 4840* (Carnegie Inst., Stanford); Siskiyou Summit, *Kildale 8246* (Stanford). CALIFORNIA. Siskiyou Co.: Lava Beds National Monument, *Applegate 9357, 9427, 9478b* (Stanford); Marble Mt., *Chandler 1680, 1697* (U. of Calif.); southeast spur, Preston

Peak, *Kildale 8607* (Stanford); south side of Shaftrock Mt., Hilt, *Rixford* (Calif. Acad.); West Fork, Cottonwood Creek, *Wheeler 2732* (U. of Calif.); Raspberry Lake, South Fork of Indian Creek, *Kildale 8692, 8716* (Stanford); South Fork of Salmon River near Big Flat, *Howell 13162* (U. of Calif.); summit of divide between Salmon River and Scott Valley, *Kildale 5487* (Stanford). Humboldt Co.: South Fork Mt., Blake Lookout, *Gillespie 10609* (Stanford).

This form occurs on Mount Ashland, which is supposedly near the type locality for ssp. *ashlandica*. The two have in common a very dense pubescence, but in other respects they are very different. Subspecies *globosa* has a very leafy-bracted inflorescence, small globose whitish flowers, in which the petals scarcely equal the short sepals, and dark brown akenes. In all these characters it differs from ssp. *ashlandica*, and no intermediates between the two have been discovered. It is evidently a distinct ecotype, although in the transplant gardens it reacts much like the montane forms of ssp. *typica*.

3k. *Potentilla glandulosa* ssp. *Ewanii* Keck subsp. nov.

Caudiculis valde elongatis tenuibus, caulibus floriferis filiformibus erectis subnudis 8–12 cm. longis a medio vel tertio superiore dichotomo-ramosis paucifloris, foliis radicalibus 2.5–5 cm. longis brevissime petiolatis hirsutis viscidulis, foliolis 7–11 orbiculari-flabelliformibus profunde inciso-serratis plerisque 4–7 mm. longis, calycibus hirsutis late campanulatis ca. 4.5 mm. longis, petalis cuneato-obovatis calyce sublongioribus. Type: *Joseph A. Ewan 2674* (Herbarium of the California Academy of Sciences), from above spring seepage near Windy Camp, Mount Islip, San Gabriel Mountains, Los Angeles County, California, at 2285 m. elevation, June 24, 1930; in late flower. Isotype, U. S. National Herbarium. Noted to be locally frequent.

Known only from the type collection, but possibly the material cited by Jepson (Fl. Calif. 2:181, 1936) from the San Gabriel Mountains, under *P. glandulosa* var. *Peirsonii*, is the same. This variety rests upon the type of *Drymocallis cuneifolia* Rydb., which we refer to ssp. *nevadensis*. The material of ssp. *Ewanii* differs from *nevadensis* and from the type of *cuneifolia* in the small stature, the small, broad, regularly toothed leaflets, the dense pubescence, and the very small flowers. However, the type of *D. cuneifolia* is fragmentary, and since neither *Ewanii* nor *cuneifolia* is well represented in herbaria

as yet, the possibility exists that the differences which now appear impressive may eventually lose importance. The styles in *Ewanii* are long and slender, a character upon which stress has been laid in *D. cuneifolia*, but as mentioned under that synonym, we have found this character to vary more or less at random.

Potentilla glandulosa var. *incisa* Lindl., Bot. Reg. 23:pl. 1973, 1837, which Rydberg raised to specific rank under *Drymocallis*, and which has been maintained by other authors as some sort of unit, is beclouded with doubt and does not stand for any of the preceding natural units (cf. Keck, Lloydia 1:83, 1939, under *Horkelia frondosa*).

INTERRELATIONSHIPS WITHIN CENOSPECIES *POTENTILLA ARGUTA*. *Potentilla arguta* ssp. *convallaria* is at the morphological and geographical hub of this cenospecies. We suspect that it is the most probable ancestral type in this complex. From it *arguta typica* may well have become differentiated in the east, *fissa* in the high Rockies, and *glandulosa glabrata* and *typica* to the westward, for there are evident morphological connections between these units. Phylogenetic speculations may be carried further to suggest that the Eurasian members of the section *Drymocallis* may find their ancestors in North America in such a unit as *convallaria*, and may have migrated westward by way of Alaska.

It appears likely, also, that the Great Basin subspecies of *P. glandulosa*, namely, ssp. *micropetala*, *arizonica*, and *pseudorupestris*, arose more or less directly from ssp. *glabrata*, and that ssp. *reflexa* and *globosa* may trace their origin to *glandulosa typica*. Still further analysis of the evidence leads to the suggestion that *glandulosa nevadensis* may have arisen from ssp. *pseudorupestris* or ssp. *glabrata*, or both; that ssp. *ashlandica* may be a relict of uncertain origin, having, however, many characteristics of ssp. *nevadensis*; that *Hansenii* probably is of hybrid origin between *nevadensis* and *reflexa*; and that *Ewanii* is a very aberrant type that possibly evolved from a similar cross.

The division of this complex into three species, *fissa*, *arguta*, and *glandulosa*, seemed the logical procedure to follow, although it necessarily left some specimens which could fall as well under one classification as another. Since these were decidedly in the minority, they were accepted as the inevitable infrequent recombinations that one may find between ecospecies.



FIG. 14. Individual hereditary variation in a population of *Potentilla glandulosa* ssp. *typica*.

The three plants were dug December 2, 1922, on Montara Mountain, San Mateo County, California, at 180 m. elevation. The specimens were taken in 1937 from plants in a uniform garden at Stanford; they were planted as divisions from propagules grown at Mather between 1923 and 1933. The individual differences are as great at Mather as at Stanford.

TYPES OF VARIATION

Before presenting the results from the varied-environment experiments, it is essential to distinguish clearly between the different kinds of morphological variation with which we have to deal. We shall therefore devote a few paragraphs to examples of morphological differences that will concern us through the remainder of this volume.

INDIVIDUAL VARIATION WITHIN ONE POPULATION. Easily visible, hereditary variations have been observed in nearly every native population of *Potentilla glandulosa* studied. An example is given in figure 14, showing three individuals of *P. glandulosa* ssp. *typica*, all originally from one natural population, as they appeared when growing without competition in a uniform garden at Stanford. The three plants are all typical of the Coast Range ecotype except for the short inflorescence in 1077-1. The variations in this case are

not due to hybridization with related but morphologically distinct forms, for no other subspecies occur within a distance of sixty-five miles. These individual differences are, of course, hereditary, and are not the result of environmental modification.

VARIATION WITHIN ONE ECOTYPE. While ecotypes are those units within species that are fitted to survive in a particular set of conditions, they are by no means uniform in genetic composition. They may, in fact, display within themselves a kind of variation that is correlated with minor differences in the habitat they occupy.

For example, *Potentilla glandulosa* ssp. *reflexa* is an ecotype that occupies the lower western slope of the Sierra Nevada. It occurs over an appreciable range of altitude, in our transect from 600 to 2100 m. The plants from the lower ranges are generally taller than those from the upper limits of distribution of the ecotype. This is illustrated in figure 15. The two plants in this figure are from 915 m. and 2100 m. elevation, but both grow in a uniform garden, so their differences are hereditary. These extreme forms within the subspecies are interlinked by a continuous series of intermediates from intervening elevations in the Tuolumne Canyon, from which the two plants pictured also came. This example illustrates the general inverse correlation between plant stature and altitude. See figure 21 for a more complete analysis.

When two variants such as those illustrated are grown in a standard environment, there are no differences in the time of flowering between them, and both promptly fail to survive at the alpine station. They represent intra-ecotypical variation associated with differences in altitude. Similar variations exist within the alpine and subalpine ecotypes of *P. glandulosa* ssp. *nevadensis*.

VARIATION WHERE ECOTYPES MEET. When two ecotypes of the same species meet at one locality, they may produce hybrid offspring. These segregate forms variously recombining the characters of their progenitors. An example is given in figure 16, showing three plants of such a population that were originally taken from one small meadow at Ockenden, Fresno County, California, at 1680 m. elevation. The plants as shown were growing side by side in a uniform garden at Mather, so obviously the differences are hereditary. The plant 1123-2 (left) and others similar to it, characterized by their open branching, small yellow reflexed petals, and late flowering, were



FIG. 15. Altitudinal variation within the foothill ecotype of *Potentilla glandulosa* (ssp. *reflexa*).

Below, plant 1092-3 from the bottom of the Tuolumne River canyon below Mather, at 915 m. elevation, and *above*, plant 1100-11 from near the head of Waterwheel Falls, in the same canyon, at 2070 m. Both plants are shown at the same scale growing in a uniform garden at Mather.

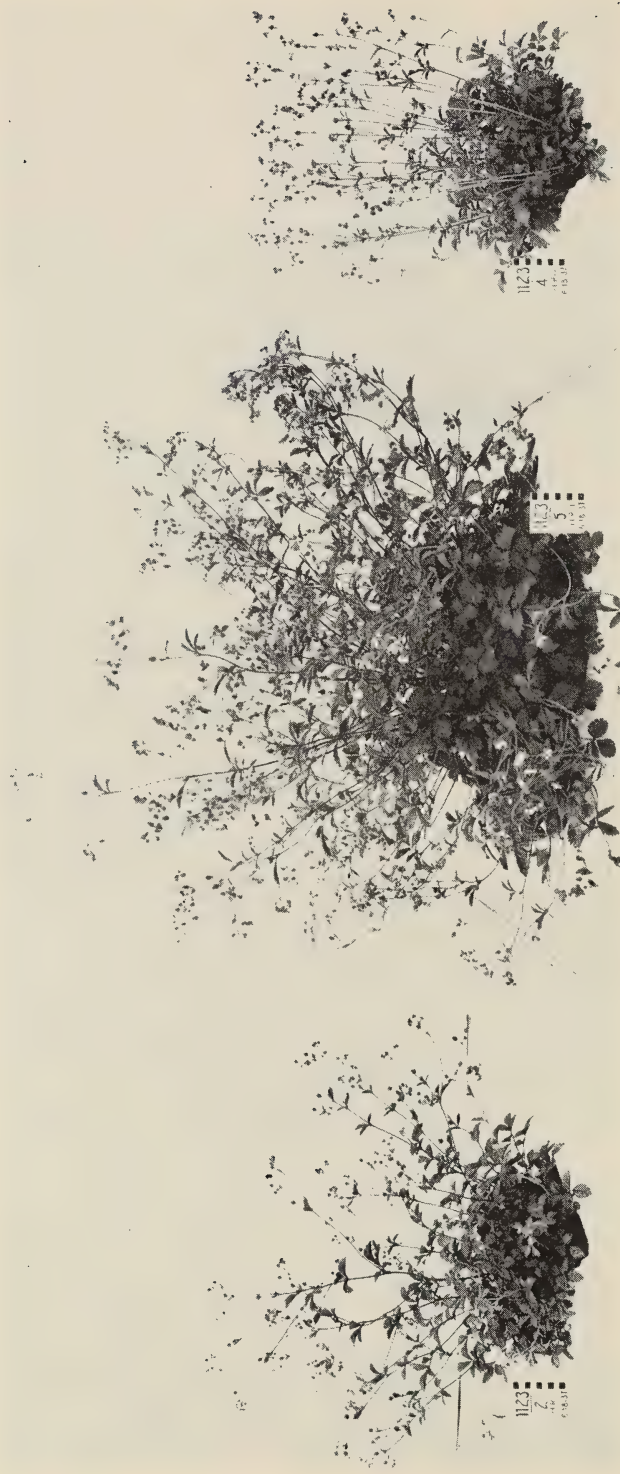


FIG. 16. Variation in *Potentilla glandulosa* where ecotypes meet.

Three transplant individuals dug July 3, 1930, from the same meadow at Ockenden, Fresno County, California, at 1680 m. elevation. Photographs taken in a uniform garden at Mather June 18, 1937: 1123-2 (left), foothill type; 1123-4 (right), alpine type; center, a probable hybrid derivative. All shown at the same scale.

found mostly on drier banks and slopes. These are referable to the foothill *P. glandulosa* ssp. *reflexa*. In moister areas plants like 1123-4 (right), with stricter stems and larger, cream white, ascending petals are found; these are referable to the alpine or subalpine ecotypes of *P. glandulosa* ssp. *nevadensis*. The plant in the center (1123-5) is intermediate in character, and probably represents a hybrid derivative. The reactions of these three individuals when transplanted to different altitudes are very different, as will be seen later.

MODIFICATIONS. All the kinds of variation discussed above are hereditary in nature. In the following pages, however, nonhereditary variations, or modifications, will be an important subject. The distinction between hereditary variations and modifications must be kept clearly in mind in order that the text that follows may be understood, because the interrelations between the two constitute one of the main theses of this volume.

One of the simplest cases is the effect of cultivation, illustrated in figure 17. The plant 1083-1 had the appearance of a dwarf in the wild, but became much taller at Stanford. Its increase in size appears to be due to the effect of cultivation and not to a change in altitude. This is evident because a clone member of the same plant became still taller in cultivation at Mather, which is approximately at the same altitude as that from which the plant came. The other plant in the figure, 1077-7, showed much less effect of cultivation. The great differences observed between the two individuals in the wild almost disappeared at Stanford.

Modifications induced by environment are superimposed on hereditary differences, so that a plant's appearance at any time is the resultant of these two distinct kinds of variation.

REACTIONS TO DIFFERENT ENVIRONMENTS

A species like *Potentilla glandulosa* is too complex a unit to consider as a whole when we propose to analyze its reactions to different environments. A preliminary study of the transplant data indicated that this species should be divided into several ecotypes—groups of individuals which react essentially alike and come from one climatic region. When the reactions to different environments are compared, the heredity must be the same, and the clone is the

basic unit. However, in order to simplify the presentation, all individuals belonging to one reaction type, or ecotype, will be considered as a group.

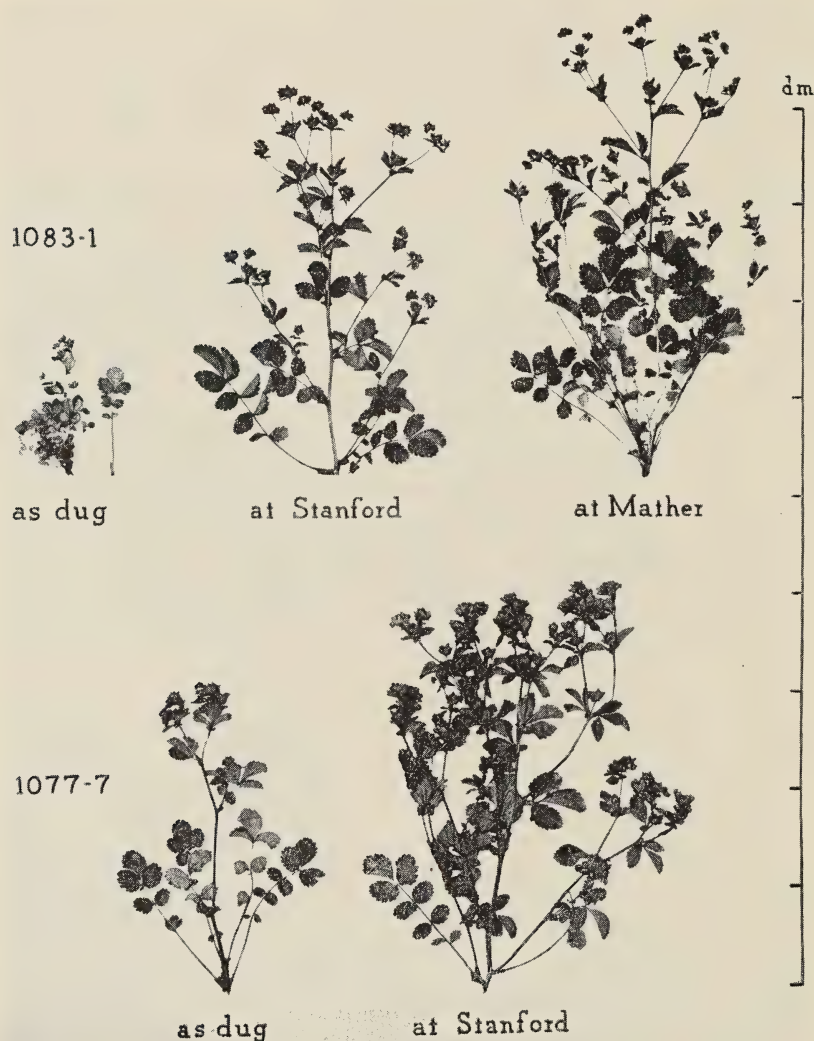


FIG. 17. Effect of cultivation on two plants of *Potentilla glandulosa*.

Plant 1083-1, from Chews Ridge, Monterey County, California, elevation 1480 m., as it appeared when dug July 24, 1934, and when grown at Stanford and at Mather in 1937. Plant 1077-7, from Montara Mountain, San Mateo County, California, elevation 180 m., as dug May 11, 1933, and at Stanford in 1935.

COAST RANGE ECOTYPE:

POTENTILLA GLANDULOSA SSP. TYPICA

The Coast Range ecotype responds to the different conditions at the transplant stations in many characteristic ways. We shall first summarize in brief review the most characteristic reactions, and then consider certain aspects in more detail. The following conclusions have been reached as a result of a careful analysis of the data available from clone members of twenty-four individuals transplanted to Stanford at 30 m., Mather at 1400 m., and Timberline at 3050 m. These general observations also apply in part to other ecotypes studied:

1. Each plant responds to the three altitudinal environments in a characteristic way, so that one can speak of a Stanford, a Mather, and a Timberline modification. In the Coast Range ecotype the differences between the Stanford and the Mather modifications are rather slight, whereas the Timberline modification is very striking.

2. Irrespective of the morphological changes induced, the individuality of every plant is retained in all its clone members after transplanting to the three altitudes, even after they have been in the new environment for as long as fifteen years.

3. While the morphological changes thus effected are mostly slight, the annual cycle of development is profoundly and immediately modified at the three stations.

4. Modification in the annual cycle of development is not sufficient to insure survival and natural development of a plant far outside of the natural range of its ecotype. It is rarely possible, for example, for the Coast Range ecotype to survive at Timberline for as long as one year, while at Mather, which is within the upper limits of the altitudinal range of this ecotype, it survives but with slightly reduced vigor.

MODIFICATION AT DIFFERENT ALTITUDES. These results are illustrated in part by the plant shown in figure 18. It came originally from the lower slopes of the Inner Coast Range. It is evident that the clone members at Stanford and Mather have much the same appearance, while that at Timberline is much reduced in stature. The individual character of the plant is retained in all three propagules, however. The clone member at Timberline survived for

three winters. This exceptional survival for a Coast Range plant was no doubt due to the fact that the winters of 1932 and 1933 were milder than average.

Closer comparison between propagules grown at Stanford and at Mather reveals small but characteristic differences. In general, the Stanford modification is taller and more robust, stems, pedicels, and leaves tend to be thicker, the glandular pubescence is more



FIG. 18. Effect of transplanting a clone of *Potentilla glandulosa* ssp. *typica* to different altitudes.

This plant, 1085-1, was dug December 4, 1929, at Mount Hamilton, Santa Clara County, California, elevation 520 m. Specimens taken: *at Stanford*, May 17, 1935, five and one-half years after transplanting; *at Mather*, June 18, 1935, five years after transplanting; and *at Timberline*, August 30, 1932, two years after transplanting.

prominent, and the color of the foliage is a dull olive green in contrast to the brighter green herbage developed at Mather. The clone members of this ecotype survive remarkably well at Mather, certain ones having continued to thrive there for the past fifteen years. One of these, originally from near the seacoast at Montara, is shown in figure 19 growing at Stanford and Mather. It failed to survive through a single winter at Timberline.

In the rare instances in which it has been possible to compare propagules at Timberline with those at Mather and Stanford, we find larger differences, as already shown in figure 18. The Timber-

line modification has shorter, more slender, and fewer flowering stems, narrower and less branched inflorescences, and correspondingly fewer flowers. However, the size of individual flowers and petals remains approximately constant.

A more detailed picture of the reactions of Coast Range plants of ssp. *typica* at the three stations is given in table 2. Measurements of selected characters are tabulated for eight typical individuals. The averages serve as an index for each character at the stations indicated.

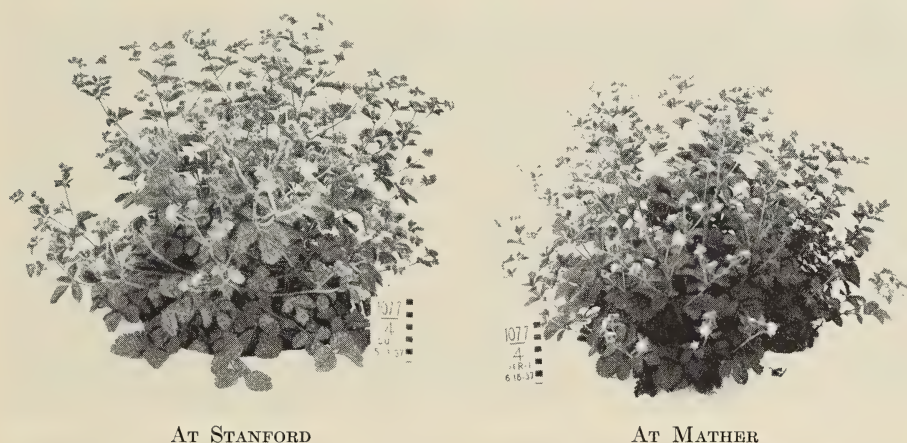


FIG. 19. A clone of *Potentilla glandulosa* ssp. *typica* at two transplant stations.

This plant, 1077-4, was dug December 2, 1922, on Montara Mountain, San Mateo County, California, at 180 m. elevation. Grown at Mather since 1923. The Stanford clone member was taken from the one at Mather in 1933. Photographs taken in 1937, shown to the same scale.

A broader picture of the situation is presented in table 3, in which the attention is focused upon three measurements which have been found throughout the transplant materials to be exceptionally favorable indices of plant behavior. These are length of longest stems, a fair measure of the size of the plant; number of flowering stems, an indication of reproductive vigor; and date of appearance of first flowers, which serves as an index to the physiological tempo of the individual. From the mass of available data, we have usually restricted statistical analysis to those three measurements, for they have proved useful indicators of plant reactions. These data are averaged from several years.

In table 3, the plants of *Potentilla glandulosa* ssp. *typica* are grouped into four classes according to their geographical origin

TABLE 2
MODIFICATIONS OF THE COAST RANGE ECOTYPE OF *POTENTILLA GLANDULOSA* SSP.
TYPICA AT THE TRANSPLANT STATIONS

Number and origin of plants	Years of data	Height (cm.)	Width (cm.)	No. stems	Stem thickness at base (mm.)	No. flowers per stem	No. nodes per stem	Longest basal leaves (cm.)	Widest basal leaves (cm.)	No. days later flowering than Stanford
AT STANFORD (30 M.)										
Mt. Hamilton:										
1085-1.....	'35	42	40	2	8.0	40-80	7-7	20.0	10.0
1085-2.....	'35-'37	38.3	36.6	2.0	5.8	50-91	6.0-7.6	18.0	7.8
Oakland Hills:										
1086-1.....	'34-'37	31.8	29.5	3.6	3.9	29-48	6.7-7.2	10.5	5.4
1086-2.....	'36	40	65	10	5.0	35-100	5-6	14.0	7.5
Montara Mt.:										
1077-4.....	'35-'37	51.3	78.3	8.0	5.5	28-98	6.3-7.0	25.0	9.2
1077-8.....	'35	42	55	8	6.5	50-100	7-7	12.0	4.5
Santa Cruz Mts.:										
1082-1.....	'35, '36	55.0	75.0	8.5	6.3	60-120	7.0-8.3	27.7	9.8
Santa Lucia Mts.:										
1083-1.....	'37	40	66	5	5.5	40-100	6-8	19.0	6.5
Average.....		42.55	55.67	5.88	5.80	41.5-92.1	6.37-7.26	18.27	7.59
AT MATHER (1400 M.)										
Mt. Hamilton:										
1085-1.....	'35	45	70	15	5.0	10-75	8-9	25.0	9.0	38
1085-2.....	'35-'37	36.3	61.3	12.3	4.3	22-78	5.3-7.0	19.7	7.5	36.6
Oakland Hills:										
1086-1.....	'34-'37	40.7	67.5	21.8	3.8	29-63	7.0-8.3	21.8	7.9	29.6
1086-2.....	'36	30	35	6	4.0	25-50	6-6	12.0	4.5	30
Montara Mt.:										
1077-4.....	'35-'37	41.0	56.3	14.0	4.2	23-62	5.3-7.3	21.7	7.3	44.0
1077-8.....	'35	35	50	5	5.0	35-150	5-8	16.0	5.5	63
Santa Cruz Mts.:										
1082-1.....	'35, '36	35	50	4.5	5.0	37-88	7.5-8.5	19.0	7.3	53.0
Santa Lucia Mts.:										
1083-1.....	'37	48	87	15	5.0	15-65	6-8	20.0	6.0	33
Average.....		38.87	59.64	11.7	4.53	25-79	6.26-7.76	19.38	6.87	40.90
AT TIMBERLINE (3050 M.)										
Mt. Hamilton:										
1085-1.....	*	18.0	18.3	4.6	2.0	12-33	6.3-7.0	8.5	3.6	91 or longer
1085-2.....	Not set.									
Oakland Hills:										
1086-1.....	Set 1930, 1933, 1934, 1935.	No survivors.								
1086-2.....	Set 1930, 1933, 1934, 1935.	No survivors.								
Montara Mt.:										
1077-4.....	Set 1934, 1937.	No survivors.								
1077-8.....	Set 1934.	No survivors.								
Santa Cruz Mts.:										
1082-1.....	Set 1934, 1935, 1937.	No survivors.								
Santa Lucia Mts.:										
1083-1.....	Set 1935.	No survivors.								

*Plant 1085-1 was set at Timberline in 1930, died and was reset in 1935, and again in 1937. Data are averaged from 1932, 1934, and 1936.

and morphological uniformity. This method of analysis aids in the detection of ecotypes within the subspecies. For example, while the California Coast Range forms are significantly taller at Stanford than at Mather, the southern Oregon plants are significantly taller at Mather than at Stanford—a complete reversal of behavior and an indication of a minor ecotypical difference.

In all classes the Mather propagules average many more flowering stems than those at Stanford. Likewise, all plants bloom first at Stanford, considerably later at Mather, and, if they survive and flower at all, much later at Timberline. The Coast Range ecotype blooms an average of 28 days later at Mather than at Stanford, and 72 days later at Timberline than at Mather, a difference of 100 days between the flowering time at Stanford and that at Timberline. Although differences might be expected from the exceedingly unlike climates, it is nevertheless striking that they are so great.

Plants originally from the same locality vary in stature and also may react differently at Stanford and Mather, as for example those from Santa Barbara and Oakland Hills. This is an indication of the genetic heterogeneity of local populations.

The time of inception of flowering is of interest when the groups of *ssp. typica* are analyzed in table 3. One observes that there is no significant mean difference in flowering time between the coastal plants of southern Oregon and those of the Coast Ranges of California. This behavior could scarcely have been predicted. On examining the members of the groups individually, we note that the two Santa Barbara plants are almost two weeks earlier than most of the rest. Other appreciable differences in individual earliness can likewise be noted.

The southern California group is nearly three weeks later in flower at Stanford than the plants from the Coast Ranges. The delay does not seem to be connected with a greater vegetative activity, for none of the plants of the southern group grows as tall as those from the Coast Ranges. It is interesting that irrespective of the earliness shown at Stanford, all these groups come into bloom almost simultaneously at Mather. This is probably connected with the fact that they are dormant at Mather in winter and all start spring growth at about the same time. At Stanford the Coast Range forms of this subspecies are in active growth all winter, while the others are more or less dormant.

TABLE 3
MODIFICATIONS IN VIGOR AND EARLINESS IN *POTENTILLA GLANDULOSA* SSP. *TYPICA*

NUMBER AND ORIGIN OF PLANTS	LATITUDE NORTH	YEARS OF DATA	LONGEST STEMS (CM.)		NUMBER OF STEMS		DATE OF FIRST FLOWERS*		
			Stanford	Mather	Stanford	Mather	Stanford	Mather†	Timberline‡
SOUTHERN OREGON: 1146-1, Rogue River, Jackson Co., 305 m. 1147-1, Grants Pass, Josephine Co., 290 m. -2, Same. -3, Same. -4, Same. Means. Mean differences. <i>t</i> =	42°25'	'35-'37	65.0	81.6	15.6	30.0	Apr. 16	May 27	(Jul. 11)
	42°25'	'35-'37	38.3	54.0	10.6	63.3	Apr. 24	May 30
	42°25'	'35-'37	51.5	54.5	11.0	24.0	Apr. 24	May 28
	42°25'	'35-'37	35.0	52.0	2.0	37.6	May 1	May 28	Aug. 20
	42°25'	'35-'37	38.6	40.3	3.0	8.3	Apr. 18	May 26	(Jul. 23)
	45.68 ±5.60	56.48 ±6.78	8.45 ±2.59	32.64 ±9.05	Apr. 22.5	May 27.8	Aug. 19.5
	Ma-St: 10.80±3.46 3.121		Ma-St: 24.19±8.74 2.768				
							
							
							
CALIFORNIA COAST RANGES: 1140-2, E. of Laytonville, 670 m.. 1086-1, Oakland Hills, Alameda Co., 200 m.. -2, Same. 1085-1, Mt. Hamilton, Santa Clara Co., 520 m.. -2, Same. 1077-1, Montara Mt., San Mateo Co., 180 m.. -4, Same. -5, Same. -8, Same. 1082-1, Santa Cruz Mts., San Mateo Co., 565 m.. 1083-1, Chews Ridge, Monterey Co., 1480 m.. 1119-1, Santa Barbara, 50 m.. -2, Same. Means. Mean differences. <i>t</i> =	39°40'	'35-'37	50.3	40.0	2.6	11.6	Apr. 29	May 28	Aug. 15
	37°50'	'35-'37	34.7	43.0	3.3	24.0	Apr. 29	May 27
	37°50'	'36	40.0	25.0	10.0	6.0	Apr. 24	May 27
	37°30'	'35	50.0	40.0	2.0	15.0	Apr. 23	May 26
	37°30'	'35-'37	41.0	38.6	2.3	12.3	Apr. 22	May 27	Aug. 25
	37°40'	'37	13.0	9.0	7.0	4.0	Apr. 10	May 27
	37°40'	'35-'37	51.0	38.3	8.3	14.0	Apr. 16	May 29
	37°40'	'35	20.0	18.0	3.0	4.0	(Apr. 25)	May 28
	37°40'	'35	42.0	35.0	8.0	5.0	(Apr. 1)	May 25
	37°35'	'35-'36	54.0	40.0	8.5	4.5	Apr. 21	June 9
	36°25'	'37	40.0	46.0	5.0	15.0	(May 1)	May 27
	34°20'	'35-'37	56.0	27.6	6.0	8.0	Apr. 9	May 31
34°20'	'35-'37	54.3	55.6	9.6	31.6	Apr. 7	May 28	
.....	42.02 ±3.64	35.08 ±3.41	5.79 ±0.65	11.92 ±2.31	Apr. 18.9	May 28.4	Aug. 20.0	
.....	St-Ma: 6.94±2.72 2.551		Ma-St: 6.13±2.25 2.724					
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TABLE 3—Continued

NUMBER AND ORIGIN OF PLANTS	LATITUDE NORTH	YEARS OF DATA	LONGEST STEMS (CM.)		NUMBER OF STEMS		DATE OF FIRST FLOWERS*		
			Stanford	Mather	Stanford	Mather	Stanford	Mather†	Timberline‡
SOUTHERN CALIFORNIA:									
Southern Sierras:									
1125-1, White River, 760 m.....	35°45'	32.0	37.0	2.0	11.0	May 10	May 28	Aug. 27
-2, Same.....	35°45'	30.0	33.0	1.0	7.0	May 11	May 27
San Gabriel Mts.:									
1139-1, Mt. Wilson, 1070 m.....	34°10'	22.0	30.0	6.0	12.5	May 12	June 1
-2, Same.....	34°10'	37.0	25.0	3.5	9.0	Apr. 23
1138-1, Barley Flats, 1710 m.....	34°10'	36.0	11.0	May 27
-2, Same.....	34°10'	33.0	30.5	6.0	13.0	May 12	May 28	Sep. 1
Means.....	30.8	31.9	3.7	10.7	May 7.6	May 29.0	Aug. 29.5
NORTHERN CALIFORNIA AND OREGON,									
MONTANE:									
Siskiyou Co., California:									
1143-1, Willow Creek Mt., 2440 m.	41°50'	45.0	39.0	1.0	3.0	May 15
Wallowa Mts., NE Oregon:									
1148-1, above Wallowa Lake, 1980 m.....	45°10'	38.3	5.5	May 28
-2, Same.....	45°10'	32.0	2.0	May 30
-3, Same.....	45°10'	38.0	43.5	2.0	7.5	May 7	May 30
-4, Same.....	45°10'	42.8	5.3	May 28
Means.....	41.5	39.0	1.5	4.7	May 11.0	May 29.3

* Fractions rounded to nearest date.

† Dates at Mather averaged from one medium early and one medium late year.

‡ Dates from Timberline principally from 1934, which was six to eight weeks earlier than 1936.

() Dates in parentheses not comparable because of recent planting or for other reasons; not included in means.

The southern California group shown in table 3 is montane, and its individuals come from higher elevations than those from the Coast Ranges. It is from the belt occupied by *ssp. reflexa*, which is equally delayed in flowering at Stanford. In other words, the morphology of these plants places them with *ssp. typica*, but their flowering reactions are those of *ssp. reflexa*. Several explanations could be offered for this behavior: one is that these plants had exchanged genes with *reflexa*; another is that they are an independent selection from the Coast Range ecotype; a third, that they are southern members of a once more extensive montane race of *typica*, all of whose members followed such a reaction pattern. A few scattered colonies of *typica* still remain in the Sierra Nevada to give some credibility to the last explanation.

The fourth group in table 3, from the mountains of northern California and Oregon, reacts the same way as the montane group from southern California. It is equally delayed in flowering at Stanford, where these plants bloom with some difficulty and do not prosper.

Therefore, in going from Grants Pass, at 42° 25' N., to Santa Barbara, at 34° 25' N., a north-south distance of approximately 550 miles, one finds forms of *ssp. typica* differing slightly from one another both in morphology and in reactions to transplanting. The differences in reaction between the most northern and the most southern plants are not great, but as we study them their reality becomes evident. All fail equally, however, when transplanted to Timberline.

CONSTANT CHARACTERS. While the size of the vegetative parts of an individual may be modified by transplanting, their basic structure is relatively constant. Thus, the number and relative lengths of corresponding internodes, the placement and angle of side shoots, the shape of bracts, stipules, and sepals, the size, color, and shape of petals, the character of the pubescence, the pattern of venation, texture, and toothing of leaves, and the individual peculiarities in the arrangement and number of leaflets and in the development of the rosette are characters that are faithfully reproduced despite transplanting to different environments. The individuality of a given plant, as expressed by a combination of such characters in the clone members, is retained. For example, the divisions of

1077-1 and -4, shown in figure 14, and grown at Mather for fourteen years, still retain their original characteristics, and are easily identified as being parts of the same individuals as those at Stanford. They have developed none of the characteristics peculiar to the plants of this species native at Mather. A great many similar examples could be cited.

SEASONAL DIFFERENCES. The contrasting climates at Stanford, Mather, and Timberline stations induce profound changes in the seasonal cycle of development. Coast Range forms are in more or less active growth throughout the year at Stanford. Late in January they produce a new crop of basal leaves in response to winter rains and rising spring temperatures. Flowering stems develop soon after, and the first flowers appear around the middle of April. By the first of June some akenes are ripe, and by July or August all the seed has been shed and the flowering stems wither. At this time the first set of basal leaves becomes senescent, and a new crop develops. From August until as late as December the plants continue to grow slowly, after which they have a short period of quiescence. This period is longest in years with the most severe winters.

At Mather, forms from the Coast Ranges begin spring growth after the last snows have melted, ordinarily in mid-April. Basal leaves and flowering stems are produced rapidly, and the first flowers appear toward the end of May. The akenes ripen by the end of June, and a month later most of them have fallen. By mid-July the basal leaves produced in early spring are replaced by a new crop, which continues activity through the first frosts until as late as the first part of November. From then on until April the plants are completely dormant.

When planted at Timberline, plants from the Coast Range are usually killed by the rigors of the first winter. If they survive, they have a growing period before them of scarcely three months—ordinarily from July 1 until late September. This interval is usually too short for them to ripen akenes, although they may manage to flower before the advent of killing frosts.

While the coastal members of *Potentilla glandulosa* begin their growth simultaneously with the alpine ecotype of the species soon after the snows melt, they produce their leaves, stems, and inflores-

cence more slowly. It is evident that they are timed to a much slower rhythm of seasonal development and to a longer season.

EFFECT OF DIFFERENCES IN LIGHT AND MOISTURE. Differences in light intensity bring about quite spectacular changes, as shown by clone members grown simultaneously in the dry sun, dry shade, moist sun, and moist shade gardens at Mather, described on page 14. The differences between sun and shade caused more visible effect than the differences in amount of moisture. This is illustrated in figure 20, by a plant originally from the hills back of Oakland.

The nature of the modifications is as follows: Dry shade, in comparison with dry sun, produces a taller plant with a more open inflorescence and greatly expanded leaves and bracts of thinner texture and darker color; petioles, peduncles, and corresponding internodes are longer, and an extra node or two may be produced on flowering stems. Moist shade, when contrasted with moist sun, shows parallel differences, the propagule in moist sun being quite similar to that in the dry sun. Clone members in dry gardens are obviously shorter and smaller-leaved, a fact correlated with the lessened vigor in the dry plots. The most extreme modifications occur in dry sun and moist shade; however, the individuality of the plant has not been lost even though its vegetative characters have been so modified that, upon superficial examination, some observers might mistake these clone members for distinct species.

Measurements made upon the individual shown in figure 20 give a further picture of the extent of the modifications observed in the water-light gardens. The results obtained from averaging measurements taken over a period of four years are given in table 4. The original data from which this summary is compiled were tabulated annually at the time vouchers were taken. Three more plants of this ecotype were also grown in the water-light gardens and showed similar reactions (table 9).

Coast Range forms of *Potentilla glandulosa* show a greater modifiability under the conditions of the water-light gardens at Mather than do the Sierran subspecies. Also, they appear to have a greater tolerance for differences in light and moisture, as reflected by their relatively vigorous condition in this set of gardens as compared with the greater variability shown by mid-Sierran and alpine sub-



FIG. 20. Modifications in a clone of *Potentilla glandulosa* ssp. *typica* in the water-light gardens at Mather. This plant, 1086-2, was dug February 7, 1926, in hills near Oakland, California, at 200 m. elevation. Propagules were set in 1927 except the one in dry shade, which was set in 1934 from a division held at Stanford. The specimens were all taken in June 1936.

species. These observations lend support to the idea of Lundegårdh (1931, p. 23) that plants which have the capacity to produce either "sun leaves" or "shade leaves" in response to the kind of environment in which they grow are able to survive both in sun and in shade, whereas plants which can produce only one kind or the other are obligate sun or shade plants, depending upon the sort produced. Lundegårdh's distinction between facultative and obligate sun and shade plants, however, may be too sharply emphasized, for we find all degrees of modification among different races of *Potentilla glandulosa* and other species in our water-light gardens.

TABLE 4
CLONE 1086-2 IN WATER-LIGHT GARDENS*

Character	Dry sun	Dry shade	Moist sun	Moist shade
Height (cm.).....	27.8	46.0	29.8	47.8
Width (cm.).....	38.0	56.0	49.5	81.8
No. stems.....	11.5	5.7	12.5	11.8
No. nodes per stem.....	5.6	6.8	6.2	7.1
Longest basal leaves (cm.).....	12.5	18.3	16.5	26.0
Widest basal leaves (cm.).....	5.8	7.6	6.5	11.0
No. leaflets.....	7-9	7-9	7-9	7-9

* Based upon four-year averages, except dry shade, which is averaged from three years.

THE ABSENCE OF A MARITIME ECOTYPE IN SSP. *TYPICA*. It is surprising that a plant like *P. glandulosa typica* that occurs so close to the coast has not developed a truly maritime ecotype. But there are indications that such an ecotype is beginning to evolve in the most exposed habitats occupied by this subspecies. Figure 14 (p. 49) illustrates this point. Six individuals were taken sixteen years ago at the exposed Montara Summit near the coast. Two of these were dwarfs similar to 1077-1 with the inflorescences barely surmounting the leaves. The other four were of the common and taller Coast Range ecotype, similar to 1077-4 and the intermediate 1077-2 in figure 14. Over a period of years the height differences have persisted. The two dwarf plants have averaged 17.5 cm. at Stanford and 14.2 cm. at Mather, in contrast with the four individuals of more usual stature, which averaged 44.8 cm. at Stanford and 37.6 cm. at Mather, a difference of 250 per cent between dwarf and tall plants. The dwarfs are not weak plants comparable to

those segregated in genetic experiments, for they have survived for the entire period at Mather in a climate outside of their natural range. If the Coast Range ecotype finally succeeds in evolving a successful maritime ecotype, it should be expected to invade the exposed maritime belt, whereas today the subspecies tends to stay back in the hills where it is protected from the strong winds.

SIERRAN FOOTHILL ECOTYPE:
POTENTILLA GLANDULOSA SSP. *REFLEXA*

The foothill ecotype of *Potentilla glandulosa* consists of plants with large rosettes, anthocyanous herbage, moderately glandular but very pubescent stems that are surmounted by openly branched inflorescences, and small, yellow-petaled flowers.

ALTITUDINAL DIFFERENCES. The foothill ecotype occurs between 250 and 2200 m. elevation, and the plants from the higher elevations are the shorter. Altitudinal near-extremes were illustrated in figure 15. It has already been emphasized (p. 50) that these differences are hereditary and not due to the environment. Figure 21 shows graphically the heights of thirty-eight individuals from the central and the southern Sierra Nevada and the lengths of their basal leaves. These are plotted from measurements made in the Mather garden. This figure shows both the hereditary differences as they appear in a uniform garden and their correlation with the elevations of the original habitats. In the Sierra Nevada, the individuals of this ecotype are largest between 900 and 1500 m. elevation, and become progressively smaller as they are found above or below this range. Since the Mather station falls within the region of maximum growth for ssp. *reflexa*, it might be supposed that the results at Stanford, below the range of the subspecies, might differ. However, measurements from Stanford show that the same picture is found there; the individuals originally from between 900 and 1500 m. are the largest, although the differences are much smaller.

MODIFICATIONS AT DIFFERENT ALTITUDES. The foothill ecotype is modified as much or even more at the three stations than the Coast Range ecotype. The appearance at the three stations of an individual originally from Mather is shown in figure 22. The modifications produced are rather parallel to those found in ssp. *typica*,

shown in figure 18. The clone member at Stanford, as contrasted with the one at Mather, has slightly coarser, wider, and darker green leaves, fewer but somewhat stouter and shorter flowering stems and peduncles, and a greater development of glands. The

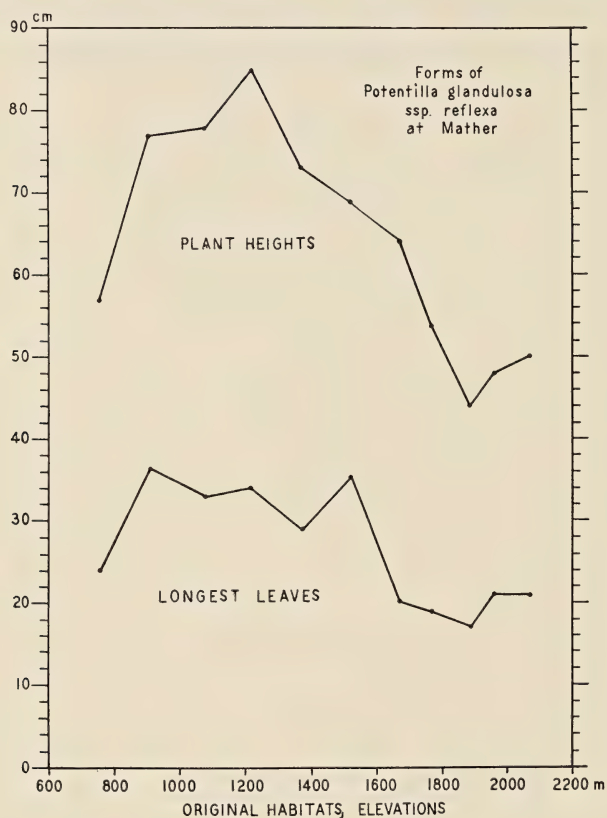


FIG. 21. *Potentilla glandulosa* ssp. *reflexa*; graph showing relation between size of plants and elevation of their original habitats.

A total of 38 plants are represented, all from the central and southern Sierra Nevada. Each point is an average value determined from from one to eight individuals in a uniform garden at Mather, at 1400 m. elevation. Data from 1937.

propagule at Mather is the tallest and most floriferous of the three. In other plants of this ecotype the modifications are even greater. At Timberline there is a marked reduction in size and number of all herbaceous parts.

From the mass of data on modifications in ssp. *reflexa*, figures on plant height and time of flowering are assembled in table 5 as an illustration of the many modifiable features. The plants are placed



FIG. 22. Modifications in a clone of *Potentilla glandulosa* ssp. *reflexa* at three altitudes.

This plant, 1093-13, was dug November 2, 1926, at Mather and propagated at Berkeley. Specimens taken: *at Stanford*, May 17, 1935; this clone member was planted at Berkeley in 1927 and moved to Stanford in 1929; *at Mather*, June 19, 1935, eight years after transplanting; and *at Timberline*, August 24, 1935, five years after transplanting, from a clone member held at Berkeley and Stanford from 1926 to 1930.

in three subgroups: one from lower, another from higher elevations in a transect across the central portion of the Sierra Nevada, and a third from the southern Sierra and the mountains of southern California. This is done in order to clarify the issue as to whether or not plants of ssp. *reflexa* represent a single ecotype.

These data show that the plants from lower altitudes are taller at Mather than at Stanford, while those from high elevations are insignificantly shorter. The few plants that managed to produce flowering stems at Timberline were in all cases dwarfer than at either of the other stations.

Flowering time of this ecotype at the three stations roughly parallels that of the Coast Range ecotype, as shown in table 3,

TABLE 5
MODIFICATIONS IN HEIGHT AND EARLINESS IN *POTENTILLA GLANDULOSA* SSP. *REFLEXA*

NUMBER AND ORIGIN OF PLANTS	YEARS OF DATA	HEIGHT OF PLANTS (CM.)			DATE OF FIRST FLOWERS		
		Stanford	Mather	Timberline	Stanford	Mather*	Timberline
FOOTHILL AND MID-ALTITUDE RACE, TUOLUMNE COUNTY:							
1091-1, Groveland, 915 m.....	'37	62	68	May 1	May 27
1092-1, Lower Tuolumne Canyon, 915 m..	'36	50	82	May 1	May 29
-2, Same.....	'36-'37	50.0	59.0	May 3	May 27
-3, Same.....	'36-'37	63.0	78.0	May 1	May 28
-4, Lower Tuolumne Canyon; 1100 m.....	'36-'37	52.5	66.0	45	May 2	May 27	Aug. 15
-5, Same.....	'36-'37	62.0	79.5	Apr. 29	May 30
-7, Lower Tuolumne Canyon, 1220 m.....	'36-'37	53.5	83.0	50	May 4	May 26	Aug. 8
-8, Same.....	'36-'37	56.0	89.5	25	Apr. 24	May 27	Sep. 10
1093-8, Mather, 1400 m.....	'35	50	50	May 15	May 29
-9, Same.....	'35-'36	57.5	67.5	Apr. 30	May 26
-10, Same.....	'35, '37	60.0	73.5	32	May 4	May 29	Aug. 25
-11, Same.....	'35	45	50	May 10	May 26
-13, Same.....	'35-'37	50.7	70.7	45	Apr. 30	May 26	Aug. 20
-14, Same.....	'35	50	95	May 10	May 26
-15, Same.....	'35-'36	31.5	61.5	May 7	May 27
-16, Mather, 1425 m.....	'35-'37	56.3	71.6	May 6	May 30
-17, Same.....	'35-'37	53.3	77.3	45	May 5	May 28	Aug. 25
Means.....		53.13	72.01 ±3.10	40.33	May 3.65	May 27.53	Aug. 22.33
Mean differences.....		Ma—St:18.88±3.22; Ma—Ti:31.68			Ma—St:22.88 days	Ti—Ma:85.80 days	
t=.....		5.868 (very significant)					
HIGH-ALTITUDE RACE, YOSEMITE NATIONAL PARK:							
1097-1, Snow Creek Trail, 1890 m.....	'35, '37	33.0	32.5	Apr. 22	May 28
1100-1, Upper Tuolumne Canyon, 1750 m.....	'36-'37	64.0	34.0	30	May 3	Jun. 7	Sep. 5
-2, Same.....	'36-'37	47.0	42.5	May 3	Jun. 8
-3, Upper Tuolumne Canyon, 1800 m.....	'36	30	30	May 1	Jun. 6
-5, Upper Tuolumne Canyon, 1830 m.....	'36	40	30	Apr. 28	May 28
-6, Upper Tuolumne Canyon, 1980 m.....	'37	39	48	Apr. 28	May 29
-7, Same.....	'36-'37	49.5	44.0	May 1	May 26
-8, Same.....	'36-'37	40.0	26.0	20	Apr. 24	May 28	Sep. 5
-9, Upper Tuolumne Canyon, 2070 m.....	'36-'37	52.5	44.0	May 1	May 28
-10, Same.....	'37	40	47	May 1	May 29
-11, Same.....	'36-'37	42.5	34.5	Apr. 28	May 28
-12, Same.....	'37	33	50	40	May 1	May 29	Aug. 9
Means.....		42.54	38.54 ±2.36	30.0	Apr. 29.25	May 30.62	Aug. 27.0
Mean differences.....		St—Ma:4.00±3.49; Ma—Ti:8.54			Ma—St:31.32 days	Ti—Ma:88.38 days	
t=.....		1.148 (insignificant)					
Difference, foothill—high-montane at Mather.....		33.47 ± 3.90			3.09 days (insignificant)		
t=.....		8.584 (very significant)					

*Dates at Mather averaged from one medium early and one medium late year.

(Continued on following page)

TABLE 5—Continued

NUMBER AND ORIGIN OF PLANTS	YEARS OF DATA	HEIGHT OF PLANTS (CM.)			DATE OF FIRST FLOWERS		
		Stanford	Mather	Timberline	Stanford	Mather*	Timberline
SOUTHERN SIERRA NEVADA AND SOUTHERN CALIFORNIA:							
1121-1, Toll House Grade, 760 m.....	'35, '37	47.5	70.0	22	May 6	May 26	(Jul. 25)
1122-1, Pine Ridge, 1525 m.....	'35-'36	40.0	75.0	34.0	May 10	May 28	Sep. 18
-2, Same.....		52.7	80.0	35	Apr. 30	May 26	Aug. 30
1123-2, Ockenden, 1680 m.....	'35, '37	21.5	59.5	28.0	May 7	Jun. 1	Sep. 20
1127-1, below Oak Grove, 760 m.....	'35-'37	45.7	69.7	(6)	Apr. 12	May 22
1129-2, Atwells, Sequoia Park, 1960 m....	'35	30	55	May 14	May 29
1131-1, below Mineral King, 2250 m.....		48.5	74.0	30.0	May 3	May 28	Aug. 31
1126-1, Greenhorn Mts., 1890 m.....	'35-'36	47.5	57.5	May 6	May 24
-2, Same.....	'35-'37	43.3	52.3	Apr. 19	May 27
<i>San Bernardino Mts.:</i>							
1137-2, N. of Santa Ana Canyon, 1370 m..		47	68.3	33.3	May 5	May 30	Sep. 3
-3, Bear Valley, 2040 m.....	'35-'37	58.7	47.3	25	May 3	May 27	(Aug. 15)
-4, Deep Creek, 1980 m.....		42	68.7	Apr. 25	May 27
<i>San Jacinto Mts.:</i>							
1136-1, Fern Valley, 1520 m.....		47.0	49.0	May 10	May 31
-2, Strawberry Creek, 1550 m.....		30.5	31.0	(10)	Apr. 20	Jun. 6	Aug. 28
-3, Banning Road, 1675 m.....		45	49.0	(10)	May 5	May 31	Aug. 28
-4, Stoney Creek, 1920 m.....		64	74.3	May 10	May 31
<i>Cuyamaca Mts.:</i>							
1135-1, North Peak, 1400 m.....		25	51.0	May 14	May 26
-2, Same.....	'35-'37	49.3	48.5	May 4	Jun. 2
Means.....		43.62	60.01	29.61	May 2.9	May 28.6	Sep. 4.9
All <i>P. glandulosa reflexa</i> : Means.....		46.78	58.40	33.71	May 2.26 ±0.93	May 28.72 ±0.50	Aug. 29.13 ±3.10

* Dates at Mather averaged from one medium early and one medium late year.

except that at Stanford flowering is one to two weeks later. The Timberline data are fragmentary, because plants of *reflexa* seldom survive one winter at that station. The general topic of survival is discussed further on page 107.

Variation among individuals is considerable, as is shown by the large standard errors. One reason for this is that they represent so many populations. Reversals of the general trend are observed in some instances, and yearly variations are appreciable, but the general picture is fairly summarized by the averages.

We find correlations, also, between the data for plant height, length of basal leaves, and number of flowering stems. The propagules at Stanford produce significantly fewer stems than those at

Mather, and the clone members at Timberline have the fewest of all. This is shown by means tabulated from four-year averages for twenty individuals at the three stations, which give for Stanford 7.8, for Mather 24.2, and for Timberline 3.1. The same individuals produced a mean maximum number of flowers per stem as follows: at Stanford 76.9, at Mather 76.6, and at Timberline 32.2. These two sets of figures may be taken as a gauge of the relative vigor of the propagules at the three stations. They show that far fewer stems per propagule are produced at Stanford than at Mather, whereas the number of flowers per stem is the same. At Timberline both the number of stems and the number of flowers per stem are reduced.

It is therefore clear that plants of the foothill ecotype are most vigorous at Mather, where the environment most closely matches that of their native habitats, and least vigorous at Timberline. At Stanford they thrive moderately well, but not as well as at Mather. Here, they are detrimentally affected by the long, rainless summers, as is indicated by their slow growth.

CONSTANT CHARACTERS. As in *ssp. typica*, the basic structural characteristics or individual peculiarities of plants of *ssp. reflexa* are not destroyed by the induced modifications, but are retained regardless of where the individual is transplanted. Details in pattern of leaf venation, arrangement of leaflets, and shape of bracts and petals are unfailingly replicated in all clone members. The number of nodes per stem, too, is quite constant, even in clone members at Timberline.

Corresponding parts of central stems from different propagules may be identified by reference to the terminal flower, which lacks a subtending bract. Comparisons between clone members grown at the three altitudes show that the relative lengths of corresponding internodes with respect to one another and to the stem as a whole remain quite constant. While the stems at Timberline have shorter internodes, these are all reduced more or less proportionately.

SEASONAL DEVELOPMENT. Like the Coast Range races, the Sierran foothill ecotype modifies its seasonal development profoundly at the three transplant stations. At Stanford the plants tend to be active most of the year, although they start their activity a little later than plants of the Coast Range ecotype; at Mather, where they

are in their normal habitat, they are dormant for six months; but at Timberline active growth is limited to a season of some ten or twelve weeks.

Spring growth commences at Stanford in February or March, and the first flowers appear during the latter part of April or early May. Fruit begins to ripen a month later, and by July the flowering stems begin to wither. New basal leaves replace the now senescent first set, and vegetative growth continues slowly until November or December, when frosts cause a short dormancy. At Mather spring growth commences somewhat later, around mid-April, when rosette leaves and young stems develop rapidly. The first flowers open in late May or early June, and by August or early September the fruit is ripe and stems begin to wither. New basal leaves appear in late summer and function until they are killed by October frosts. At Timberline the first growth does not appear until July 1, and flowers are barely able to open before frosts kill them in late August or mid-September.

Excepting 1127-1, from Oak Grove in the foothills of Tulare County, which at Stanford is three weeks earlier than the average, the plants of the foothill ecotype are remarkably uniform as to earliness, and the standard errors are small, especially that of the Mather modification (table 5). The plants from high elevations form no exception to this general rule. It is worth noting that at Mather even 1127-1 is not appreciably earlier than the others.

SIERRAN MID-ALTITUDE MEADOW ECOTYPE:
POTENTILLA GLANDULOSA SSP. HANSENI

In the region about the transplant station at Mather, two ecotypes of *Potentilla glandulosa* are found. On the warm, drier slopes that often drain into meadows one meets the expansive but small-flowered ssp. *reflexa*. Within the meadows themselves grows the strict-stemmed ssp. *Hansenii*, with relatively large, cream-colored flowers. It is a taller, less glandular and anthocyanous plant than *reflexa*. As shown in the map (fig. 13), it is much more restricted in range than *reflexa*, and is known to occur only between 1200 and 1800 m. elevation. Ssp. *Hansenii* is evidently very closely allied to the sub-alpine ecotype of ssp. *nevadensis*, but true intergrades between the two have not yet been found.

VIGOR AND SURVIVAL. This meadow ecotype, like ssp. *reflexa*, is most vigorous and survives best at Mather, where it is in its native environs. Of great interest, however, is the fact that it is definitely better able to survive at Timberline than *reflexa*. Thus, three individuals out of six in culture have been living for eight years at the alpine station; another lived for four years, while two others survived three winters. This is in marked contrast with the survival records of transplants of *reflexa*, in which the average life is less than a year, as shown in figure 41. At Stanford, the meadow ecotype does not become nearly as vigorous, nor does it survive as well as at Mather, but, like the Sierran foothill ecotype, it grows quite successfully if irrigated.

One expression of vigor is plant height, which has been tabulated annually at the three stations. A statistical measure of this expression is given by the following mean heights in centimeters, averaged on one to four years' data, for six plants of this ecotype originally from Mather:

	Stanford	Mather	Timberline
Mean heights.....	70.37	87.80 \pm 6.33	45.72

ALTITUDINAL MODIFICATIONS AND THEIR REVERSIBILITY. In 1922, five typical individuals of the meadow ecotype, which averaged a meter in height, were dug at Mather and moved to Porcupine Flat (elevation 2440 m.), where the climate is intermediate between that of Mather and Timberline. Four of the plants lived and thrived and, although their structural characteristics remained unchanged, their stature was reduced. The records from 1924, 1926, and 1929 show that these plants reached a height of from 52 to 71 cm., with a proportional reduction in size of basal leaves. There is no indication that the size of these plants was progressively reduced during the period, 1924 to 1929, when they were at Porcupine Flat; the heights in 1924 were the same, within the expected limits of yearly variation, as in 1929. Therefore, there is no evidence of cumulative environmental effect.

After seven years at Porcupine Flat, these plants were transferred in 1929 to Timberline, at 3050 m. elevation. Here they became only 20 to 55 cm. high, with proportional decreases in the dimensions of all herbaceous parts. In 1933 vegetative divisions were made for all three stations. As soon as the propagules were

established at Mather, they became as tall and robust as the originals when dug there in 1922, while the portions at Timberline continued to show the dwarfed character. Figure 23 shows a clone as its members appeared in 1937. Figure 28 shows the same clone in four environments. Three other individuals reacted the same way.

So, these tall, robust plants from Mather became reduced in stature at Porcupine Flat, and still more so subsequently at Timberline, but they resumed their original aspect immediately upon their return to Mather after living ten years at these higher altitudes. The modifications illustrated in figure 23, therefore, are strictly reversible and dependent upon the immediate environment.

SEASONAL REACTIONS. The meadow ecotype, like the other forms discussed, is greatly affected in its seasonal cycle by altitudinal changes. Its development at the three stations is similar to that described for the Sierran foothill ecotype. Despite the fact that it survives better at Timberline (for as long as eight years), it still develops too slowly there to enable it to produce even fully opened inflorescences during the short growing period. This is illustrated in figure 23, in which the flowering stems are immature although the photograph was taken in September, just before winter weather began.

A notable seasonal difference exists between the meadow and foothill ecotypes native at Mather. The former is consistently about one month later in flowering at Stanford and two weeks later at Mather and Timberline, but matures its fruit so much more rapidly that both races have ripe akenes at about the same time. Therefore, the meadow ecotype requires more time to develop its vegetative system in spring, but takes less time to produce mature akenes.

The six plants of the meadow ecotype whose mean heights at the three stations were given on page 74 show the following spread in the mean dates of their first flowering, calculated on the same years of observation as the heights:

	Stanford	Mather	Timberline
Mean date of first flowers...	May 29.4 \pm 3.68	June 11.8 \pm 1.69	Sept. 7.8 \pm 4.76

FOOTHILL AND MEADOW ECOTYPES IN WATER-LIGHT GARDENS. It will be recalled that *Potentilla glandulosa* ssp. *typica*, from the Coast



FIG. 23. Modifications in a clone of *Potentilla glandulosa* ssp. *Hansent* at three altitudes. This plant, 1093-5, was dug September 11, 1922, at Mather, at 1409 m., brought to Porcupine Flat at 2500 m., and grown there until moved up to Timberline in 1929; propagules taken from it in 1933 were planted at Stanford and Mather in 1934 and 1935, respectively. The three photographs, shown at the same scale, were taken in the summer of 1937 (see also fig. 28).

Ranges, becomes taller and produces much larger leaves in shaded gardens than in full sun (fig. 20). Both ssp. *reflexa* and *Hanseni* behave differently in this respect; ssp. *Hanseni* is tallest in the sun gardens (fig. 37, p. 106), whereas ssp. *reflexa* shows no such pronounced modifications, although leaves are thinner and flowers fewer in the shade. Figure 24 shows a typical clone of ssp. *reflexa* in this series of gardens.

The two subspecies native at Mather also differ from each other in regard to the number of flowering stems produced in the water-light gardens (cf. table 9, p. 96). Both develop more stems in the sun than in the shade gardens, but *Hanseni* grows most vigorously in the moist sun, not quite so well in the dry sun, and has least vigor in the shade plots, although even in these it is quite healthy. Ssp. *reflexa* thrives far better than *Hanseni* in the dry sun, does almost as well in the moist sun, and better than *Hanseni* in the shade plots, although it is less vigorous there. These reactions are in line with the ecologic preferences observed in the natural distribution of these ecotypes. The foothill ecotype, *reflexa*, occurs not only on rather dry, pine-covered slopes, but also on the borders of moist meadows, and shows a wide tolerance to the varying conditions of the water-light gardens. The meadow ecotype, on the other hand, which is restricted to moist situations, thrives by far the best in the garden most like its natural environment, having a more restricted tolerance of other conditions.

SUBALPINE AND ALPINE ECOTYPES:

POTENTILLA GLANDULOSA SSP. NEVADENSIS

Sierra Nevadan representatives of this subspecies are found from well above timber line at 3500 m., down the western slope to a line roughly varying between the 1600- and 2100-m. level. Despite differences in stature and minor features, these are so completely interconnected by morphological intermediates that taxonomic division of the group appears impossible. Nevertheless, results from transplanting indicate that two ecotypes can be distinguished. These have been separated for statistical treatment on the basis of their differences in behavior. With few rare exceptions, this separation corresponds roughly to the elevations of the original habitats. The



FIG. 24. A clone of *Potentilla glandulosa* ssp. *reflexa* in the water-light gardens at Mather. This plant, 1131-1, was dug July 7, 1930, near Mineral King, Tulare County, California, at 2250 m. elevation. All four propagules were at Stanford until planted at Mather in 1933. The specimens were taken at Mather in June 1935.

plants from higher elevations, which are the earliest and smallest, are classed as alpinos, those from lower elevations as subalpinos.

Plants of the subalpine ecotype hybridize at times with those of *ssp. reflexa* in localities where the two grow near each other (cf. fig. 16). No definite hybrids are known from nature, however, between either ecotype of *nevadensis* and the comparatively rare *Hanseni*, probably because such hybrids are impossible to detect morphologically. We have not had the opportunity of studying a population of *Hanseni* in close proximity to one of *nevadensis*, but doubtless such situations exist.

MODIFICATIONS. The subalpine ecotype of this subspecies is modified more than any other form of *Potentilla glandulosa* that we have tested, except *ssp. Hanseni*. These two have also a great capacity to adapt themselves to the climates of the transplant stations and they can survive at all three. The alpine ecotype survives also at all stations, although it is least prosperous at Stanford. Examples of modifications in clone members of the subalpine and alpine ecotypes are shown in figure 25. It is evident that the subalpine plant has been altered most strikingly, although the changes in the alpine are of a similar nature.

If one compares the clone members of the alpine and subalpine plants as they grow side by side at Timberline, one is impressed by their superficial similarity. If the subalpine plant had merely been moved to Timberline and compared with the natives near by, it would not be difficult to conclude that it had been transformed into an alpine form by its environment. Yet, when one compares both races in three environments, it is evident at once that they are different entities; they differ in capacity for modification, in earliness, and in morphology. The changes induced in individuals of the subalpine and alpine ecotypes shown in figure 25 are seen in greater detail in the herbarium specimens of figure 26.

The changes that result from transplanting to the three altitudes involve, primarily, the alteration in size of herbaceous parts. At Timberline, as compared with Mather, stems are fewer, shorter, and thinner, and bear fewer flowers; leaves are fewer and, together with the bracts, are much reduced in length and width. At Stanford, as compared with Mather, stems likewise become shorter and fewer, and also often thicker, but the number of flowers per stem is, on

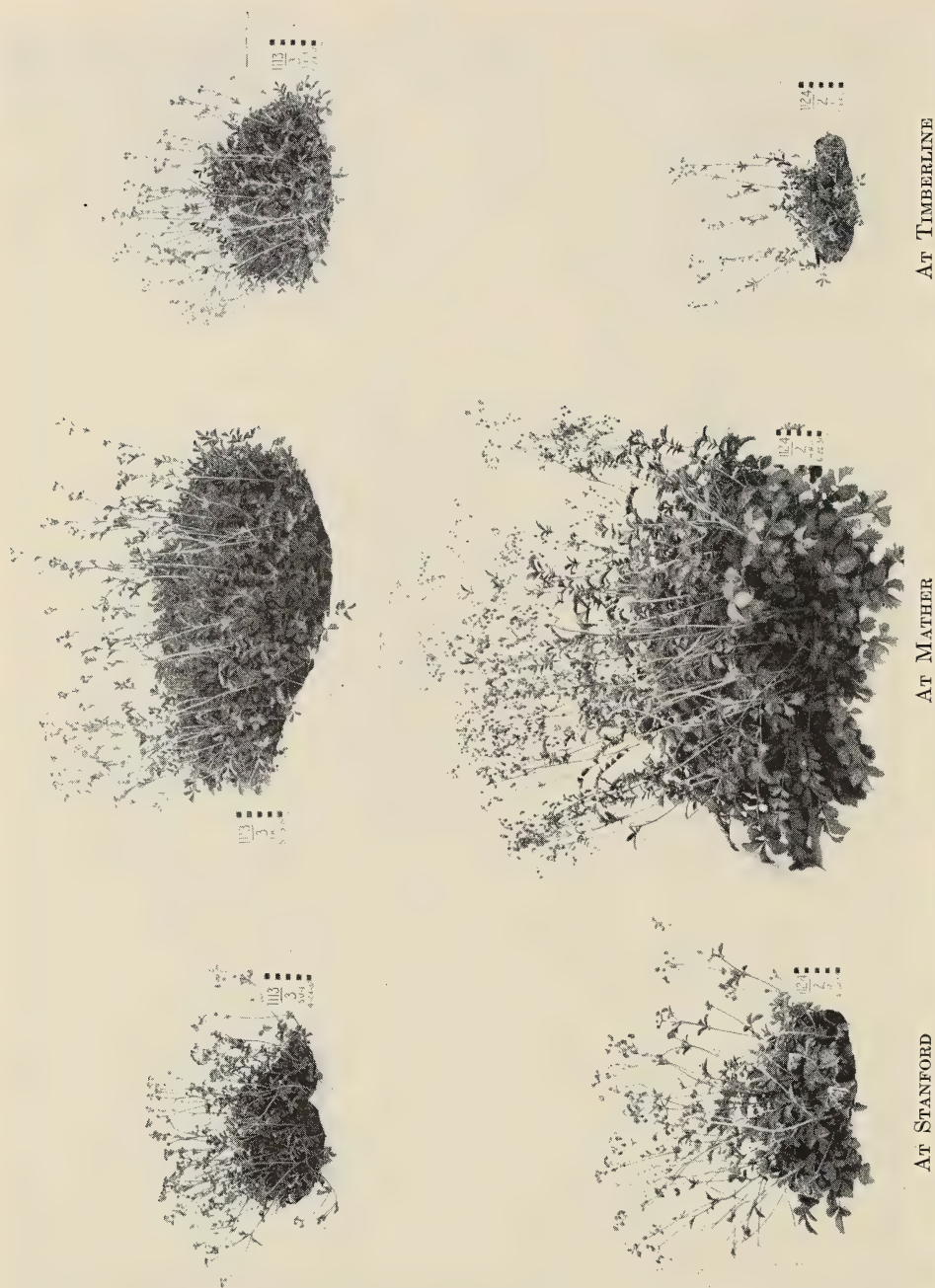


FIG. 25. Modifications in clones representing the alpine and subalpine ecotypes of *Potentilla glandulosa* ssp. *nevadensis*.
 Above: the alpine 1113-3, dug September 12, 1929, near Timberline station, at 3050 m. The propagules were planted at Mather and Timberline in 1930 and at Stanford in 1934. Below: the subalpine 1124-2, dug July 3, 1930, near Shaver Lake, Fresno County, California, at 1770 m. The propagules were planted at Mather and Timberline in 1931 and at Stanford in 1934. All photographs were taken during the summer of 1937, shown to the same scale.

an average, the same; leaves and bracts are smaller, and fewer leaves are produced.

The numbers beside the modifications of the subalpine plant in figure 26 indicate corresponding nodes in the clone members, which were numbered from the rosette to the terminal flower on the main axis. The basic arrangement of the three sets of nodes is similar, although the length of internodes and the amount of branching varies at the three altitudes. The additional two nodes on the Mather propagule are somewhat unusual, for there is usually the same number of nodes on the central shaft of all clone members at the three stations.

There are individual differences in capacity for modification in both the subalpine and the alpine ecotypes. These are greater in the subalpine, which is the more heterogeneous. This is evident from tables 6 and 7, in which height of plants and date of first flowers are tabulated for the subalpine and alpine ecotypes, respectively. In preparing these tables it was soon discovered that the plants could not be assigned to ecotypes on the basis of the elevations of their original habitats, their stature, or any other single character. However, differences at Timberline in resistance to freezing, earliness of flowering, speed of the ripening process, and vigor mark the natural boundaries between these two ecotypes. If a plant was tall and late flowering, it was classed as subalpine; if it was short, early flowering, and able to ripen akenes at Timberline, it was classed as alpine. But several combinations of these characters have been found, such as plants of medium height that are late in flowering, forms that are early but not markedly frost-resistant, and plants from subalpine elevations behaving as alpine. Their final classification was determined by considering all factors, especially their ability to reproduce at Timberline.

Considering first the subalpine ecotype: it was found to follow a reaction pattern similar to that of plants of *ssp. reflexa* from low elevations, as regards both height and flowering time. The plants are tallest at Mather, intermediate at Stanford, and shortest at Timberline, and they flower nearly 23 days earlier at Stanford than at Mather, and nearly 86 days earlier at Mather than at Timberline.

In table 7 we see that the alpine ecotype follows a reaction pattern closely parallel to that of the subalpine ecotype. The chief dissimilarities are that the alpine ecotype is less modifiable in stature,

1113-1



1124-2



FIG. 26
(Legend on opposite page)

and that its time of flowering averages two weeks earlier at Stanford and Timberline and one week earlier at Mather. Since the standard errors for the measurements of this character are small, the differences in flowering time are very significant. The remarkable control exerted upon plants of different heredity by the climate is brought out by the fact that the mean difference in time of flowering between Stanford and Timberline is 108.0 days for the subalpine ecotype and 107.9 days for the alpine despite their consistent differences in earliness at both stations.

Another interesting comparison to be noted in tables 6 and 7 is that at Timberline the mean heights of the two races are not very different, but at Stanford and especially at Mather more marked differences occur. At Timberline, individual differences frequently bring a plant of one ecotype into the height class of the other. This means that the effect illustrated in figures 25 and 26, in which the subalpine forms may simulate the alpine through modification, is of common occurrence. It is equally obvious, however, that the two races are nevertheless of distinctly different hereditary composition.

SEASONAL DEVELOPMENT. Like the previously considered ecotypes of *Potentilla glandulosa*, the alpine and subalpine ecotypes adjust their seasonal cycle to accord with the climates of our three stations. Alpine plants, whose period of active growth is but three or four months in their native environs or in the garden at Timberline, remain green for nine months or longer at Stanford, where they ordinarily rest in dormancy only from mid-November to mid-February. At Mather, growth continues for six months or longer, from approximately the first of April to the first part of October.

Subalpine plants follow essentially the same seasonal cycle as alpine forms, the principal difference being that the alpiners flower and ripen fruit one to two weeks earlier. It is this characteristic that enables alpine plants to complete their full seasonal cycle at

FIG. 26. Modifications at three altitudes in clones representing the alpine and subalpine ecotypes of *Potentilla glandulosa* ssp. *nevadensis*.

Above: the alpine 1113-1, dug September 12, 1929, near Timberline station. The propagules were planted at Mather in 1930 and at Stanford and Timberline in 1934 from divisions held at Stanford. The specimens shown were taken in 1935. *Below:* the subalpine 1124-2, from Shaver Lake, is also shown in figure 25, which see. Specimens taken in 1937. The numerals along the stems indicate the number of nodes.

TABLE 6

MODIFICATIONS IN HEIGHT AND EARLINESS IN *POTENTILLA GLANDULOSA* SSP. *NEVADENSIS*,
SUBALPINE ECOTYPE

(Averages from three years, 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	HEIGHT OF PLANTS (CM.)			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather*	Timberline
NORTHERN SIERRA NEVADA:						
1142-1, Westwood, Lassen Co., 1525 m...	40.7	62.0	25.0	Apr. 27	May 19	Aug. 7
-2, Same.....	23.7	65.0	May 17	May 20
-3, Same.....	23.7	59.0	24.3	May 12	May 20	Aug. 21
-4, Same.....	33.5	64.7	18.5	May 7	May 20	Aug. 24
-5, Same.....	30.0	62.0	32.0	Apr. 30	May 20	Aug. 12
CENTRAL SIERRA NEVADA:						
1096-1, Dark Hole, Yosemite, 2440 m....	35.5	71.7	29.0	Apr. 29	May 26	Aug. 31
-2, Same.....	34.5	66.0	26.0	Apr. 25	May 25	Aug. 22
-3, Same.....	42.5	41.5	45.0	Apr. 25	May 26	Aug. 18
-4, Same.....	46.5	78.7	40.7	May 7	May 26	Aug. 16
-6, Same.....	39.5	43.0	27.3	Apr. 20	May 24	Aug. 28
-7, Harden Lake, Yosemite, 2300 m..	47.5	57.5	52.3	Apr. 29	May 26	Aug. 13
1098-1, Porcupine Flat, Yosemite, 2500 m.	38.5	53.0	24.7	May 9	May 27	Aug. 30
-2, Same.....	44.5	53.0	May 2	May 26
-5, Same.....	42.3	74.3	48.3	May 2	May 28	Aug. 11
-6, Same.....	68.0	44.7	May 27	Aug. 13
-7, Same.....	25.0	70.7	May 10	May 26
-8, Same.....	37.0	73.7	35.3	May 9	May 27	Aug. 8
1099-1, Yosemite Creek, Yosemite, 2190 m.	31.0	51.0	Apr. 18	May 21
1101-1, Tenaya Lake, Yosemite, 2415 m...	44.0	42.0	20.0	Apr. 25	May 23	Aug. 22
SOUTHERN SIERRA NEVADA:						
1123-4, Oekenden, Fresno Co., 1680 m...	28.5	57.5	26.3	Apr. 26	May 24	Aug. 4
-5, Same.....	67.0	94.3	27.0	Apr. 30	May 26	Aug. 29
1124-1, Shaver Lake, Fresno Co., 1770 m.	66.0	81.7	40.0	Apr. 30	May 27	Aug. 23
-2, Same.....	64.5	80.7	35.0	May 2	May 25	Aug. 3
-3, Same.....	90.0	May 26
-4, Same.....	77.7	May 22
-5, Same.....	61.0	97.0	35.0	May 6	May 28	Aug. 15
Means.....	41.17	66.76 ±2.98	32.82	May 1.6 ± 1.42	May 24.4 ± 0.56	Aug. 17.5 ± 1.94
Difference between means.....	Ma—St:25.59±2.87; Ma—Ti:33.94±3.86			Ma—St:22.8 days; Ti—Ma:85.1 days		

* Averaged from one medium early and one medium late year.

TABLE 7
MODIFICATIONS IN HEIGHT AND EARLINESS IN *POTENTILLA GLANDULOSA* SSP. *NEVADENSIS*,
ALPINE ECOTYPE
(Averages from three years, 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	HEIGHT OF PLANTS (CM.)			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather*	Timberline
CENTRAL SIERRA NEVADA:						
<i>Yosemite Park:</i>						
1100-13, Glen Aulin, Tuolumne River, 2375 m.	34.5	52.0	27.5	Apr. 19	May 18	Aug. 12
-14, Same.....	42.5	49.5	27.5	Apr. 19	May 18	Aug. 5
-15, Same.....	36.5	31.0	20.0	Apr. 20	May 27	Aug. 10
-16, Same.....	30.5	36.5	28.0	Apr. 20	May 23	Aug. 6
-17, Delaney Creek, Tuolumne River, 2560 m.....	26.5	40.5	Apr. 20	May 23
1109-1, Tuolumne Meadows, 2740 m.....	20.0	30.3	Apr. 18	Jul. 31
-2, Same.....	29.0	52.7	37.0	Apr. 15	May 16	Jul. 26
-4, Same.....	38.0	59.0	39.7	Apr. 22	May 16	Jul. 31
-5, Same.....	32.5	29.5	30.3	Apr. 18	May 20	Aug. 6
1114-2, Mt. Dana, 3185 m.....	30.0	57.0	21.7	Apr. 18	May 22	Aug. 7
-7, Mt. Dana, 3290 m.....	21.0	38.3	29.0	Apr. 12	May 16	Jul. 31
-8, Same.....	38.0	May 16
<i>Mono County:</i>						
1113-1, Slate Creek, 3050 m.....	30.7	31.0	34.0	Apr. 17	May 16	Jul. 31
-2, Same.....	21.5	43.0	24.0	Apr. 14	May 16	Jul. 31
-3, Same.....	31.0	50.0	35.7	Apr. 13	May 19	Jul. 30
-4, Same.....	33.0	52.7	29.3	Apr. 12	May 16	Jul. 31
-5, Same.....	27.5	59.3	23.5	Apr. 6	May 16	Aug. 10
-6, Same.....	20.5	42.3	34.0	Apr. 4	May 14	Aug. 4
-7, Slate Creek, 3260 m.....	27.0	42.7	24.3	Apr. 5	May 16	Aug. 4
-8, Same.....	34.7	12.7	May 19	Aug. 7
-9, Same.....	(18)	40.0	11.7	May 18	Aug. 6
-10, Same.....	(20)	39.7	17.0	May 15	Jul. 31
1116-2, Leevining Canyon, 2925 m.....	23.0	38.5	28.5	Apr. 17	May 17	Jul. 31
-3, Leevining Canyon, 2740 m.....	26.0	50.0	31.3	Apr. 10	May 18	Aug. 4
SOUTHERN SIERRA NEVADA:						
1132-1, Mineral King, Tulare Co., 2390 m....	41.5	54.0	27.3	Apr. 26	May 16	Aug. 3
-2, Same.....	29.5	58.7	29.7	May 10	May 18	Aug. 7
-3, Same.....	30.0	59.3	May 16
-4, Same.....	22.0	55.3	20.7	May 4	May 18	Aug. 3
-5, Same.....	47.3	22.7	May 16	Aug. 10
1134-1, Upper Monarch L., Tulare Co., 3240 m.	30.3	20.7	May 11	Jul. 28
-2, Same.....	37.3	23.7	May 11	Jul. 30
Means.....	29.34	45.00 ±1.74	26.49	Apr. 17.4 ±1.35	May 17.4 ±0.60	Aug. 3.4 ±0.82
Differences between means.....	Ma—St:15.66±2.68; Ma—Ti:18.51±1.95			Ma—St:30.0 days; Ti—Ma:78.0 days		

* Averaged from one medium early and one medium late year.
() Not included in mean.

Timberline, whereas the subalpine usually fail to mature fruit, although in some individuals part of it ripens before killing frosts come. Other physiological differences, such as resistance to cold, and general vigor in an alpine environment, may also be of importance in determining the natural distribution of the two ecotypes, for we have often observed that alpine races are distinctly more vigorous at Timberline than the subalpine. We are nevertheless convinced, from repeated observations, that a rapid rate of seasonal development is of utmost importance for survival in alpine climates.

VIGOR. By referring again to figure 25, the reader will observe that both ecotypes are most vigorous at Mather. Even the alpine plants are more vigorous at this middle altitude than where they are at home. Also, the alpine form is more robust at Timberline than the subalpine, although both are healthy. Neither is luxuriant at Stanford, but the subalpine forms thrive somewhat better than the alpine. Several of the alpinas and some of the subalpinas seldom flower here but survive as rosettes. Both ecotypes are attacked by rusts, mildews, leaf curl, and the strawberry crown-borer at Stanford to a much greater extent than at Mather or Timberline, and are, in general, more susceptible to disease than the other ecotypes of the species. Stanford's dry summers are detrimental to these moisture-loving high-montane types, even when irrigation is supplied, but the mild winter may be equally detrimental, for many come out of their period of dormancy in a visibly weakened condition.

The number of flowering stems produced and the number of flowers per stem serve as good indices of relative vigor. The following tabulations are the mean numbers of stems and of flowers per stem produced by the subalpine and alpine ecotypes based on two-year averages; fifteen individuals of the subalpine, and sixteen of

	NUMBER OF STEMS			NUMBER OF FLOWERS PER STEM		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline
Subalpine ecotype:						
Means.....	6.83	44.70	7.66	53.46	59.00	13.36
Differences between means	37.87 \pm 8.98		37.04 \pm 8.97	5.54 \pm 6.22		45.64 \pm 5.42
Alpine ecotype:						
Means.....	12.71	38.87	12.75	27.16	34.78	14.28
Differences between means	26.16 \pm 5.99		26.12 \pm 5.00	7.62 \pm 5.44		20.50 \pm 2.71

the alpine ecotype are included in the means. The differences between the means and standard errors are also given.

It is noteworthy that the number of stems is much increased at Mather for both the subalpine and alpine ecotypes, and the number of flowers per stem is significantly increased at both Mather and Stanford. At the alpine station inflorescences are simplified and flowers reduced in number through a reduction in the number and length of side branches.

It is of much ecological interest that alpine plants should be more vigorous at the mid-altitude station, Mather, than in their native environs, Timberline. This implies that alpine forms of *Potentilla glandulosa* are capable of living at mid-altitudes as well as or even better than in higher altitudes. Their absence from the native flora at lower elevations probably means that they are less able to compete for existence in this environment than the larger mid-Sierran races. Since the latter are unable to endure the climate of higher altitudes, the alpinists may find in those habitats a place where they can compete successfully.

Why should both alpine and subalpine plants be most vigorous and produce the greatest bulk of material at Mather? This question will have to remain unanswered until suitable physiological studies have been made. It may be suggested, however, that the greater growth at Mather as compared with that at Timberline is a logical result of the longer growing season, which enables the plants to synthesize more carbohydrates and hence produce more bulk. At Stanford, indeed, the growing season is longer than at Mather, but here the average daily temperatures are higher. This would increase respiration, so that the difference between the total material synthesized and that respired might be much less than in the cooler temperatures of Mather. As will be seen later, however, there are some alpine species the clones of which decrease in size when transplanted to Mather but increase at Stanford.

LOCAL ENVIRONMENTAL DIFFERENCES AT TIMBERLINE. Local differences in slope exposure at Timberline are sufficient to produce appreciable effects on the height and vigor of transplants. Two gardens have been developed at Timberline, the large Interstation garden in a meadow on the floor of Slate Creek Valley, and a smaller plot less than 200 m. away on a southeast slope 50 m. higher in

elevation. This slope is occupied by a little forested island of vegetation, which usually is native at about 2500 m. elevation in the Sierras, but here occurs at an elevation of between 3000 and 3200 m. This suggests that the slope garden is in the midst of a distinctive microclimate. The meadow plot is frequently whitened by frost during July and August on mornings when the slope is frost-free. The slope area, which is almost horizontal in itself, is protected from extreme winds by trees and cliffs, and has an outlet through a ravine which permits cold air to drain down to the meadow. The soil in the two plots appears to be approximately the same.

In table 8 are listed six clones of the subalpine and ten of the alpine ecotype that have been grown at Mather and in both the meadow and the slope garden at Timberline. The modifications listed are computed from annual tabulations during a five- to six-year period (the same period as that covered in the graphs, fig. 31). It is very evident from this table that alpine and especially subalpine plants expand in height in the slope garden, the latter about 78 per cent as compared with clone members in the Timberline meadow. Some of the plants become almost as tall on the Timberline slope as at Mather, as for instance the alpinines 1109-4 and 1134-1. Other plants expand little or not at all. In this manner the ratio changes markedly from one individual to the next, an indication that a complex of physiological factors is operating.

Two examples of such reactions are shown in figure 27, one of an individual of the alpine ecotype from Timberline and one of a subalpine ecotype. Specimens of each clone growing at Mather are shown for comparison. A further illustration is given in figure 28, in which the reactions of the meadow ecotype, *P. glandulosa* ssp. *Hanseni*, are depicted in four environments. It is noticeable from this figure that even though the slope plant is rather tall, it fails to develop an open inflorescence like the Stanford and Mather clone members. A graphic representation of these differences is given in figure 29. It is based on data from eighteen plants of three ecotypes.

If the propagules on the Timberline slope approach the Mather modifications in stature, they nevertheless do not approach them in earliness. On the average they are even slightly later on the slope than in the Timberline meadow garden. A check on records shows that although they start spring growth one to two weeks earlier on the slope than in the meadow, they are often later coming

TABLE 8
MODIFICATIONS AT TIMBERLINE MEADOW AND SLOPE GARDENS IN
POTENTILLA GLANDULOSA SSP. NEVADENSIS
(Data averaged for period between 1932 and 1937)

NUMBER AND ORIGIN OF PLANTS	HEIGHT OF PLANTS (CM.)			DATE OF FIRST FLOWERS		
	Mather	Timberline Meadow	Slope	Mather*	Timberline Meadow	Slope
SUBALPINE ECOTYPE:						
1096-1, Dark Hole, 2440 m.....	67.8	28.0	40.0	May 26	Aug. 21	Sep. 5
1123-4, Oekenden, 1680 m.....	46.8	24.0	45.5	May 22	Aug. 2	Aug. 6
-5, Same.....	83.4	29.7	37.8	May 26	Aug. 21	Aug. 16
1124-2, Shaver Lake, 1770 m.....	78.8	33.8	51.5	May 24	Aug. 2	Aug. 6
1142-3, Westwood, 1525 m.....	59.4	21.8	34.3	May 21	Aug. 14	Aug. 17
-4, Same.....	57.4	18.5	35.6	May 21	Aug. 11	Aug. 14
Means.....	65.6	22.9	40.8	May 23.2	Aug. 11.9	Aug. 15.9
ALPINE ECOTYPE:						
1109-4, Tuolumne Meadows, 2740 m.....	59.0	38.6	54.0	May 12	Jul. 31	Jul. 25
1113-3, Slate Creek Valley, 3050 m.....	44.2	31.6	35.2	May 12	Jul. 31	Aug. 4
-5, Same.....	51.6	24.7	37.0	May 13	Aug. 3	Aug. 4
-6, Same.....	37.5	34.0	28.0	May 14	Jul. 30	(Aug. 15)
-8, Slate Creek Valley, 3260 m.....	33.6	12.4	25.0	May 20	Aug. 4	Aug. 9
-9, Same.....	35.2	12.0	17.3	May 19	Aug. 4	Aug. 7
-10, Same.....	33.8	15.2	19.8	May 19	Jul. 30	Aug. 3
1132-4, Mineral King, 2390 m.....	51.6	19.2	40.2	May 18	Aug. 2	Jul. 28
1134-1, Upper Monarch Lake, 3240 m.....	29.8	19.0	27.7	May 14	Jul. 27	Jul. 28
-2, Same.....	35.0	20.2	22.0	May 15	Jul. 28	Jul. 22
Means.....	41.1	22.7	30.6	May 15.4	Jul. 31.4	Aug. 2.0

* Flowering dates for Mather averaged for one medium early and one medium late year only.

() Not included in mean.

into flower because they attain greater size. Figure 31 shows that there are annual differences in this respect. In 1934 the plants in the slope garden were in flower considerably earlier than plants in the meadow, but during the other years they were later.

Time of flowering is evidently governed by very intricately balanced physiologic processes that respond to a complex of environmental and internal factors. The external factors include the time of

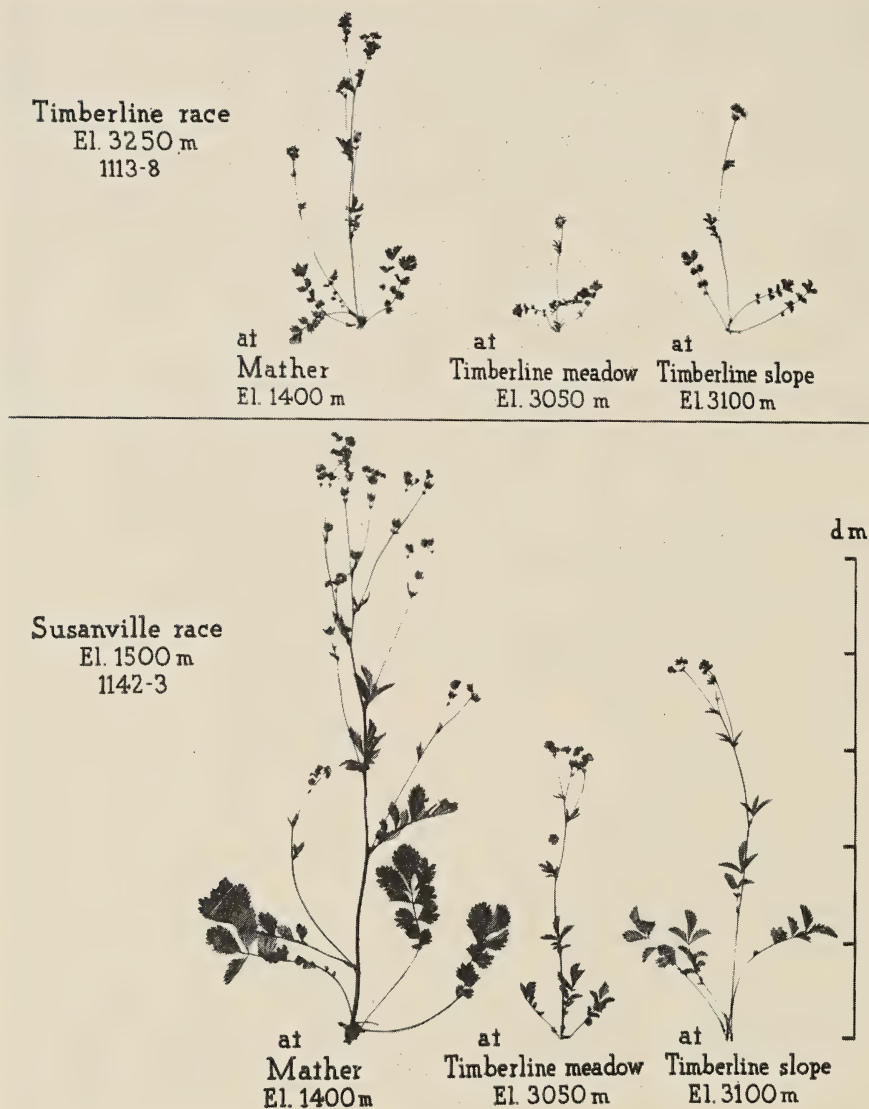


FIG. 27. Effect of local habitat differences at Timberline as compared with the effect of a major difference in altitude on clones of alpine and subalpine *Potentilla glandulosa* ssp. *nevadensis*.

Above: the alpine 1113-8, dug July 24, 1930, from above Timberline station, at 3260 m. Below: the subalpine 1142-3, dug July 23, 1930, from between Westwood and Susanville, Lassen County, California, at 1525 m. All propagules of both were planted in 1931, and the specimens shown were taken in 1935.



FIG. 28. Effect of major differences in altitude and minor differences in habitat at Timberline on a clone of *Potentilla glandulosa* ssp. *Hansenii*.

This plant, 1093-5, was dug at Mather September 11, 1922, taken to Porcupine Flat at 2500 m. until 1929, then moved to Timberline slope. In 1933 it was moved into the Timberline meadow garden. Propagules taken from it were planted at Stanford in 1934 and at Mather in 1935. The specimens were taken in 1937 at Stanford and Mather, in 1935 at Timberline meadow, and in 1932 at Timberline slope. (See also fig. 23.)

melting of the snows and the threshold temperature for starting activity; the internal include the speed of vegetative growth attained and the bulk of vegetative substance to be produced before flowering can begin under prevailing conditions.

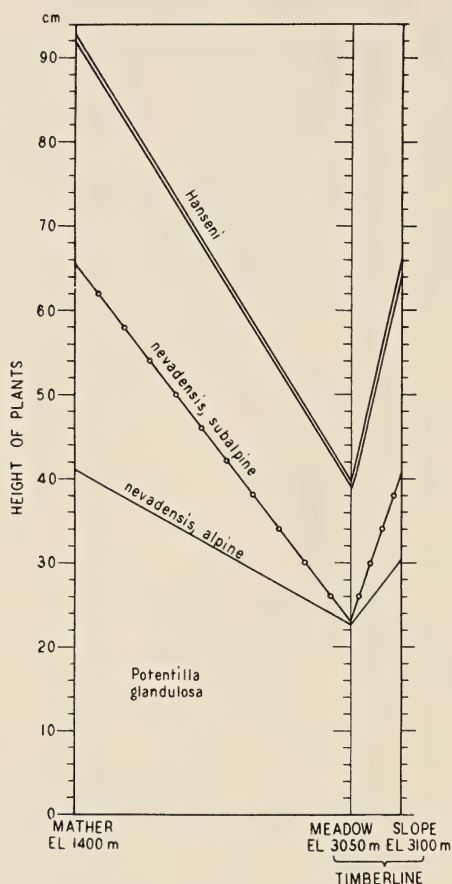


FIG. 29. Modifications in heights of clones representing three ecotypes of *Potentilla glandulosa* at Mather, and in the meadow and slope gardens at Timberline.

Data graphed are averaged from observations made between the years 1932 and 1937, on 9 plants of alpine *nevadensis*, 7 of subalpine *nevadensis*, and 2 of *Hansenii*.

YEARLY FLUCTUATIONS IN FLOWERING TIME. The gross environmental factors that may be summed up in the term "weather," such as precipitation, temperature, and sunshine, vary from year to year, and this is reflected in plant growth. Taking an easily determined stage in plant development, such as the date of opening of first flowers, we find a marked fluctuation from one year to the next.

Related plants are affected to about the same degree by annual fluctuations in the environmental factors determining the inception of the reproductive processes. This is shown in figure 30, in which the dates of first flowering are plotted for individuals of both alpine and subalpine ecotypes at Mather for five years. In the same figure, means are plotted for the ecotypes as a whole. It is clear that 1934 was an early year for flowering, and that the alpine ecotype is ordinarily several days earlier than the subalpine, and in 1934 even one month earlier. It is interesting to note that very few days separate the time of flowering of different members of one ecotype in any particular year.

Similar data obtained from plants in the Timberline slope garden are plotted in figure 31, in which figure, also, the means are plotted for each of the ecotypes in both slope and meadow gardens at Timberline. As the reader compares these graphs with those in figure 30, he will note that 1934 was an exceptionally early year at Timberline as well as at Mather, but that 1936, as compared with 1935 and 1937, was late at Timberline but early at Mather. This indicates that local instead of general conditions within a region such as the central Sierra Nevada may at times be controlling factors governing plant reactions.

EFFECT OF WATER-LIGHT GARDENS. Alpine and subalpine races of *Potentilla glandulosa* grow typically in moist, sunny meadows or slopes. Gardens most nearly approaching these conditions at Mather are most favorable to their growth. In brief, vigor is greatest in the moist sun garden, poorest in dry shade, and moderate in dry sun and moist shade. Flowering is usually appreciably reduced in the shade, as shown by fewer stems and fewer flowers per stem.

In table 9 are listed the reactions of three characters in the four gardens of the water-light variation. These characters are plant height, number of stems, and date of first flowers. Almost all the data represent four-year averages. Individual plants of the various ecotypes of *P. glandulosa* are listed here for comparisons within one ecotype and between the ecotypes. The comparison between ecotypes is summarized in the graphs presented in figures 37 to 39.

The data from the two ecotypes of *ssp. nevadensis* show that the

modifications usually associated with shading, such as larger and thinner leaves and longer and weaker stems, are not nearly so great as in coastal forms, but the weakening effect of shade is evidenced by the higher mortality. So, while the modifications are less pronounced in high-altitude forms, the tolerance to varying amounts of light and moisture is also less. The usual delay in flowering in

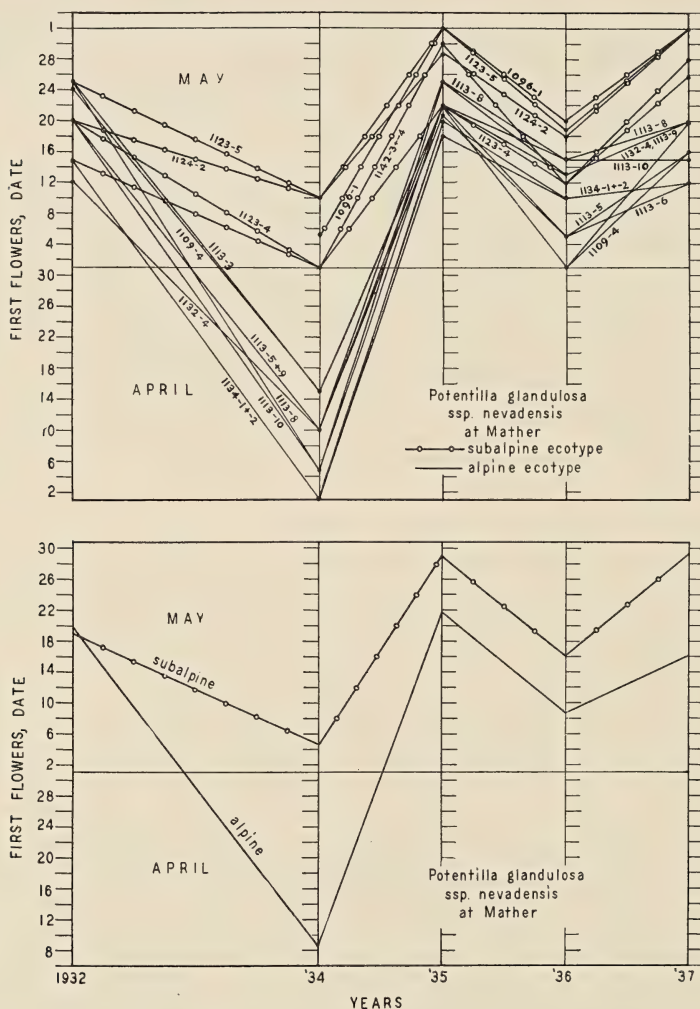


FIG. 30. Yearly variation in earliness at Mather of clones representing subalpine and alpine ecotypes of *Potentilla glandulosa* ssp. *nevadensis*.

Above: records of individual transplants for the years indicated. Below: the mean dates of flowering of the subalpine and alpine ecotypes, obtained by averaging the values for the individuals represented in the upper graph.

moist shade is very evident in the two ecotypes of *nevadensis*. Typical reactions in the water-light gardens are shown by a subalpine clone from Yosemite Park (fig. 32).

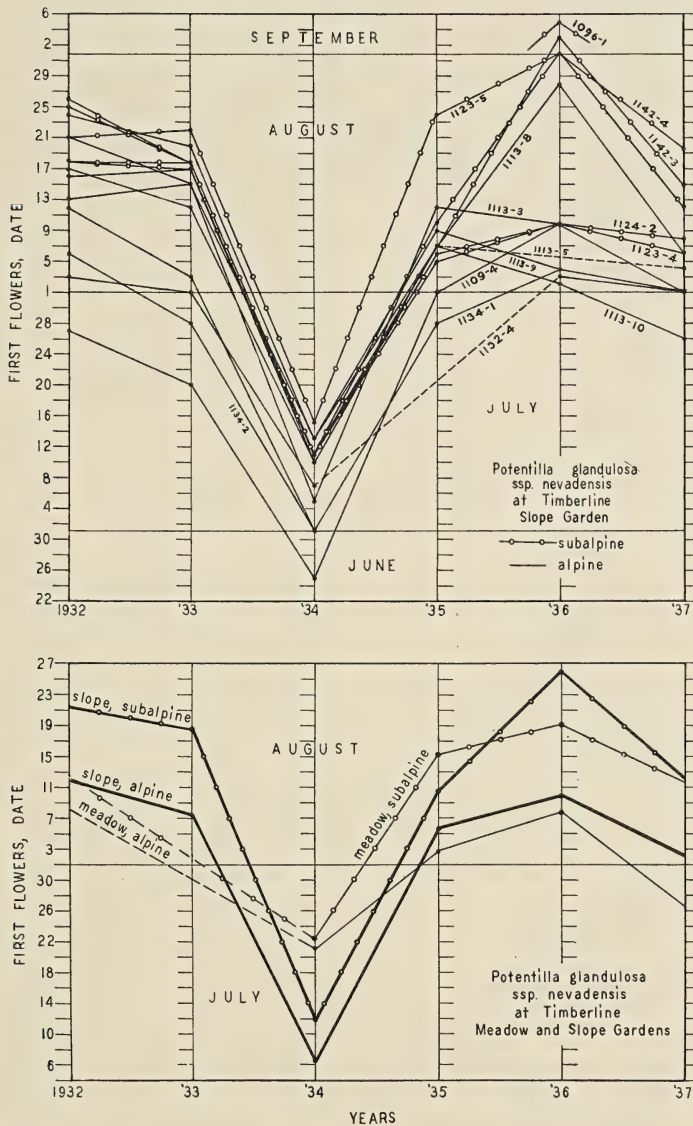


FIG. 31. Yearly variation in earliness at Timberline of clones representing subalpine and alpine ecotypes of *Potentilla glandulosa* ssp. *nevadensis*.

Above: records of individual transplants in the slope garden. Below: mean dates of flowering in the meadow and slope gardens, obtained by averaging the values for the individuals in each garden.

TABLE 9

EFFECT OF DIFFERENCES IN MOISTURE AND LIGHT ON ECOTYPES OF *POTENTILLA GLANDULOSA*
(Averages mostly from four years, 1934 to 1937)

PLANT NUMBER	HEIGHT OF PLANT (CM.)				NUMBER OF STEMS				DATE OF FIRST FLOWERS			
	DSu	DSh	MSu	MSh	DSu	DSh	MSu	MSh	DSu	DSh	MSu	MSh
COAST RANGE ECOTYPE (ssp. <i>typica</i>):												
1077-4.....	22.7	45.3	30.0	37.0	4.0	8.3	9.0	5.0	May 30	May 31	May 31	Jun. 5
-5.....	13.0	26.0	20.0	8.0	5.0	7.0	Jun. 1	May 31	May 30
1085-2.....	21.5	33.3	33.5	37.0	5.5	2.8	10.5	3.0	May 30	May 31	May 28	(May 20)
1086-2.....	27.8	47.7	31.0	47.8	11.5	5.7	12.5	11.8	May 29	Jun. 1	May 26	Jun. 4
Means.....	21.3	38.1	28.8	40.6	7.3	5.5	9.8	6.6	May 30.1	May 31.1	May 28.8	Jun. 4.5
FOOTHILL ECOTYPE (ssp. <i>reflexa</i>):												
1093-15.....	53.3	55.8	47.8	55.3	42.5	20.3	33.8	21.0	May 29	May 30	May 26	Jun. 6
1127-1.....	54.0	51.8	57.0	56.5	28.5	11.0	20.5	19.5	May 26	May 25	May 24	May 30
1129-2.....	57.0	46.0	36.7	35.0	Jun. 1	May 26
-3.....	34.3	35.0	40.3	27.0	5.3	3.0	12.3	4.0	May 30	Jun. 2	May 25	Jun. 9
1131-1.....	58.0	58.8	64.3	68.5	19.3	14.3	30.0	24.5	May 30	May 31	May 29	Jun. 6
Means.....	51.3	50.4	51.1	51.8	26.5	12.2	26.3	17.3	May 29.2	May 29.8	May 25.6	Jun. 4.5
MEADOW ECOTYPE (ssp. <i>Hanseni</i>):												
1093-1.....	97.7	54.3	101.5	91.0	13.3	4.0	28.0	6.0	Jun. 14.5	Jun. 15	Jun. 16	Jun. 19.5
SUBALPINE ECOTYPE (ssp. <i>nevadensis</i>):												
1096-1.....	58.3	40.5	74.0	64.0	23.0	7.0	14.0	13.3	May 28	May 29	May 23	Jun. 6
1098-7.....	64.3	55.8	70.8	70.3	11.8	3.5	11.8	5.8	May 29	May 29	May 25	Jun. 1
1123-5.....	82.3	47.3	56.0	69.0	15.0	4.3	25.0	10.3	May 28	May 29	May 31	Jun. 5
1124-2.....	77.3	64.8	75.0	72.8	46.3	14.3	65.0	29.3	May 26	May 26	May 23	May 29
1142-3.....	49.5	40.5	49.3	59.5	37.8	9.5	50.0	29.5	May 26	May 29	May 26	Jun. 1
Means.....	66.3	49.8	65.0	67.1	26.0	7.7	33.2	17.5	May 27.1	May 28.1	May 25.4	Jun. 1.9
ALPINE ECOTYPE (ssp. <i>nevadensis</i>):												
1109-4.....	49.3	40.5	43.0	46.3	17.7	8.8	9.0	21.7	May 22	May 24	May 19	May 29
1113-5.....	53.7	32.7	48.7	41.3	43.3	3.3	41.7	8.0	May 21	May 22	May 12	May 29
-6.....	25.3	22.0	35.3	23.3	11.7	4.0	35.0	3.0	May 18	May 12	May 25
-8.....	31.7	31.3	30.7	17.3	37.3	12.3	May 20	May 14	May 27
-10.....	30.3	19.3	31.3	31.0	14.7	3.8	60.0	26.0	May 18	May 19	May 11	May 24
1132-4.....	45.7	32.3	41.5	12.0	2.8	17.0	May 17	May 25	May 19
1134-1.....	17.0	31.0	28.3	7.0	45.0	8.0	May 24	May 11	May 28
Means.....	38.0	27.3	34.7	33.5	18.1	4.8	33.6	13.2	May 19.1	May 22.7	May 13.5	May 26.8
SSP. <i>globosa</i> (SISKIYOU MTS.):												
1144-1.....	24.5	43.3	48.0	34.7	12.8	13.3	36.8	7.0	May 27.5	May 28.5	May 26.0	May 29.5
SSP. <i>arizonica</i> (UTAH):												
1149-1.....	51.3	42.3	54.3	48.3	9.3	3.0	36.0	7.7	May 25.0	May 26.0	May 21.0	May 30.0

DSu = dry sun; DSh = dry shade; MSu = moist sun; MSh = moist shade.
() Not included in mean.

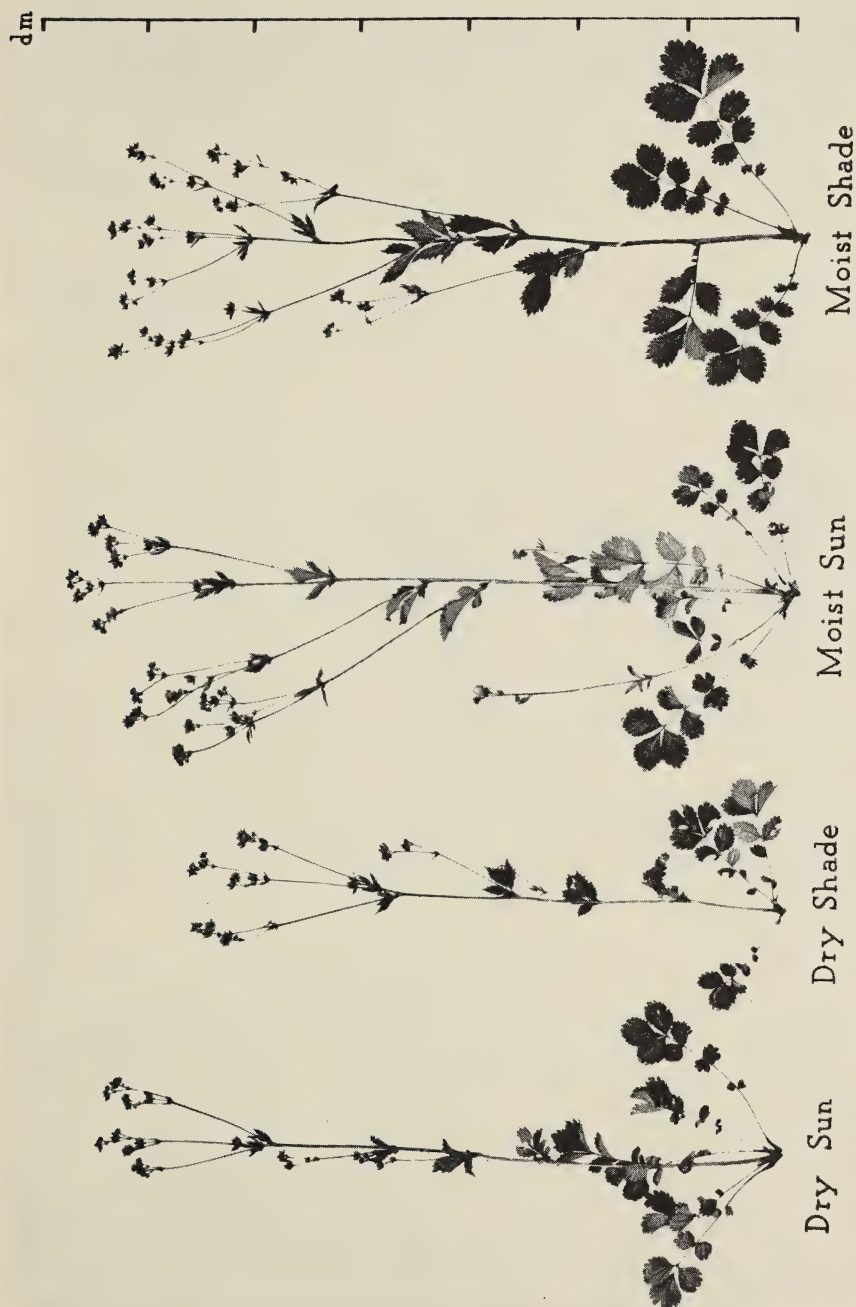


FIG. 32. Effect of the water-light gardens at Mather on a clone of subalpine *Potentilla glandulosa* ssp. *nevadensis*. This plant, 1098-7, was dug July 31, 1927, at Poreupine Flat, Yosemite Park, at 2500 m. elevation. The propagules were planted in 1933, having been held in a nursery at Stanford. These specimens were taken in June 1936.

POTENTILLA GLANDULOSA SSP. GLOBOSA

This ecotype is almost limited to the Siskiyou Mountains of northern California and adjacent Oregon, as shown in the map (fig. 13). Its members have many morphological features in common with *ssp. typica*. Its modifications in the transplant gardens are also rather parallel to those of *typica*, as shown by an average clone in figure 33. The reactions at the three stations are tabulated



FIG. 33. Modifications in a clone of *Potentilla glandulosa* ssp. *globosa* at three altitudes.

This plant, 1144-1, was dug near Siskiyou Pass, Jackson County, Oregon, September 29, 1930, at 1280 m. elevation. The propagules were planted at Mather and Timberline in 1931, and at Stanford in 1934. The specimens were taken at Stanford in 1937, at Mather in 1935, and at Timberline in 1932.

below. This ecotype is very low in stature at all stations and the inflorescences are quite congested. Its earliness at Stanford corresponds to that of the montane and Sierran races of *typica*. At Timberline it promptly dies. For its reactions in the water-light gardens see table 9.

POTENTILLA GLANDULOSA SSP. ARIZONICA

Interesting transplant data have been obtained from *P. glandulosa* ssp. *arizonica*, from Puffer Lake, Beaver County, Utah, at 2750 m. elevation. This form behaves very similarly to the subalpine ecotype of *ssp. nevadensis*. Unlike *ssp. globosa*, it increases very much

in height at Mather and survives indefinitely at Timberline, where it is as early as the subalpine ecotype of *ssp. nevadensis*. For reactions in the water-light gardens at Mather, see table 9. Some of the modifications in the interstation gardens are listed below.

	PLANT HEIGHT (CM.)			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline
Subspecies <i>globosa</i> (average of three plants for two to three years)....	23.4	29.3	20	May 6.7	May 27.2	(Sep. 1)
Subspecies <i>arizonica</i> , plant 1149-1 (three-year averages).....	28.0	46.3	23.3	Apr. 19.0	May 24.0	Aug. 25.5

OTHER SPECIES RELATED TO *POTENTILLA GLANDULOSA*

Some data have been gathered on the behavior of *Potentilla arguta* *ssp. typica* in the Stanford and Mather gardens. The material came from Rock Creek, south of Colorado Springs, Colorado, at 1830 m. elevation. It grows well at Mather, but poorly at Stanford. The lack of stolons in this species makes it difficult to divide, and for want of propagules it has not been tested at Timberline. It is shown in figure 9 (p. 28).

Seedling cultures of four races of *Potentilla rupestris* L. have been grown, namely, two from the vicinity of Gothenburg, Sweden, one from Müncheberg-Mark, Germany, and one from Kew Gardens, England, of unknown source. Thirty plants of each of the first three races and about ten of the last one behaved essentially alike. Very few of these plants would flower in the Stanford garden, or in the greenhouses and lathhouse. Those that did flower developed thin, spindly stems and divaricately branched inflorescences very different from the stout-stemmed plants with condensed inflorescences that characterize the species in Europe. Two of the best plants grown at Stanford are shown in figure 10 (p. 29), where they may be compared with the plant from a rocky, openly forested slope at Gärdsås, north of Gothenburg, from which the seeds were taken. Most of the other seedlings that flowered had a much shorter, almost scape-like inflorescence, but all had the characteristic large, pure-white petals that distinguish *rupestris* from *glandulosa*.

INDIVIDUAL DIFFERENCES IN CAPACITY FOR MODIFICATION

In the preceding pages a discussion of the reactions of *Potentilla glandulosa* has been simplified by limiting consideration to the ecotype as a whole. The picture becomes more complex as one studies the individual differences found within an ecotype.

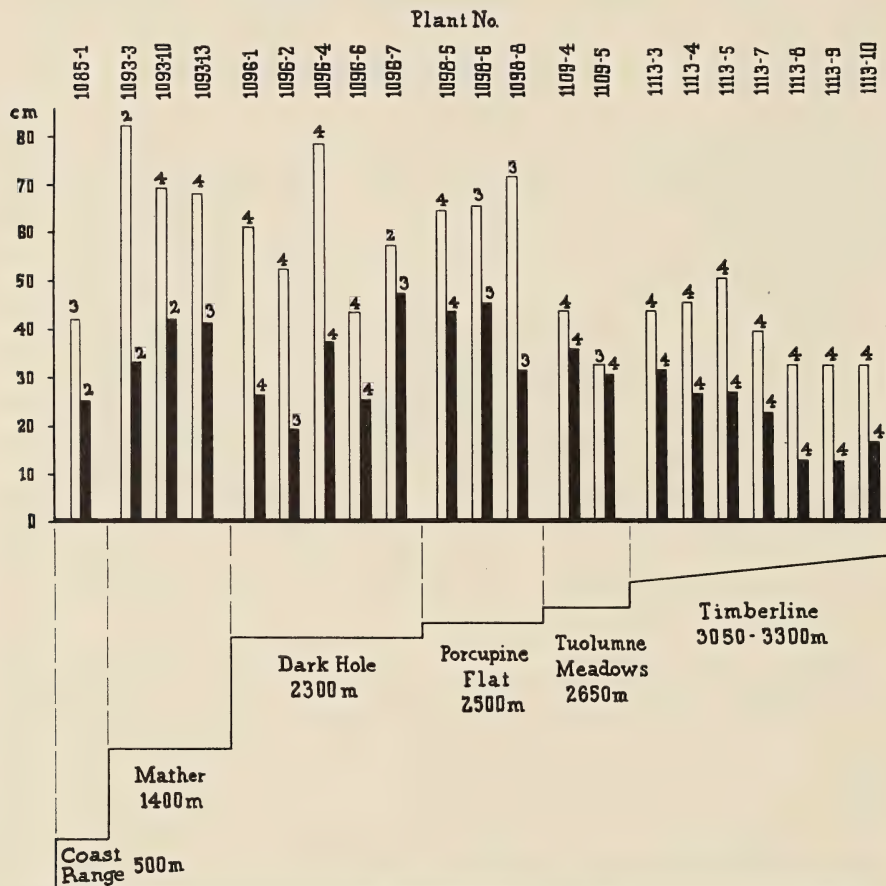


FIG. 34. Heights of clone members of *Potentilla glandulosa* at Mather (white columns) as compared with those at Timberline (black columns).

Each pair of columns represents one individual. The numerals above each column indicate the number of years averaged in determining the heights. The original localities and their elevations are also indicated.

A sample of this complexity is presented in figure 34, which shows in graphic form modifications in height of a series of plants from the transplant transect when grown at Mather and Timberline. Several facts are brought out in this figure: (1) All plants tend

to show a reduction in height at Timberline as compared with Mather; (2) a difference in modifiability is exhibited by individuals originally from the same elevation; (3) a marked variation in height is observed within one population; (4) plants native at the highest elevations tend to be the smallest, and those at mid-altitude the tallest; and (5) the complexity within the local population and ecotype is magnified as we consider the species as a whole.

Among the plants native at Dark Hole, 1096-4 becomes dwarfed to a much greater degree at Timberline than does 1096-7. Similarly, of the plants originally from Timberline, 1113-8 and -9 are increased in height at Mather more than 1113-3, while 1113-10 shows an intermediate degree of enlargement. Finally, 1109-5, from Tuolumne Meadows, shows no appreciable difference between its Mather and Timberline modifications. Plants from another transect behave in the same manner.

The modifications in height are usually correlated with changes in other characters, such as size of leaves, density of pubescence, extent of branching in the inflorescence, number of flowers per stem, and differences in texture. The data for heights, therefore, also apply in general to modifications in other characters.

Since individual variation includes not only differences in morphology, but also differences in the capacity for modification, it is essential to study a number of individuals before reaching conclusions concerning the effect of changed environment upon a species. The statistical tables contain many examples of individual differences in capacity for modification.

ECOTYPE DIFFERENCES IN POTENTILLA GLANDULOSA

A direct comparison between the various ecotypes of this species brings to light the magnitude of the racial differences between them. Data have been gathered annually or oftener on more than two dozen characters, involving many prominent features of form and function, from all plants in the experiments wherever possible. There have been chosen for illustration here two simple but significant tabulations for the races grown at the three stations, namely, height of plants, and date of first flowers.

Figure 35 shows the relative heights at the three stations of eight races of *Potentilla glandulosa*. The tallest form at all three stations

is the Sierran mid-altitude meadow ecotype, ssp. *Hanseni*, and the shortest form is ssp. *globosa*. The other three subspecies mentioned in detail in the preceding pages, *typica*, *reflexa*, and *nevadensis*, are divided into two parts each; in the case of *typica*, principally on

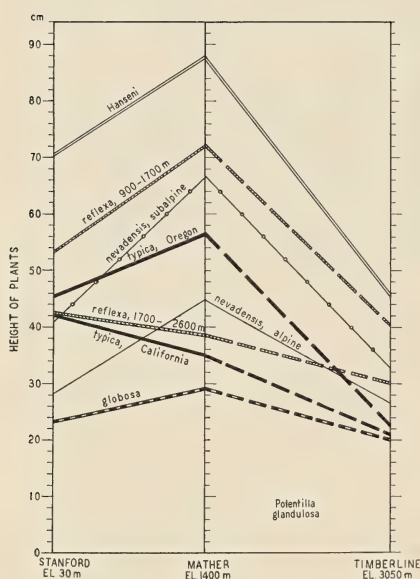


FIG. 35

Modifications in height at three altitudes in clones representing ecotypes of *Potentilla glandulosa* (fig. 35) and in their dates of first flowers (fig. 36).

The graphs are constructed for the plants listed in tables 3 to 7 from data averaged for the years 1935 to 1937.

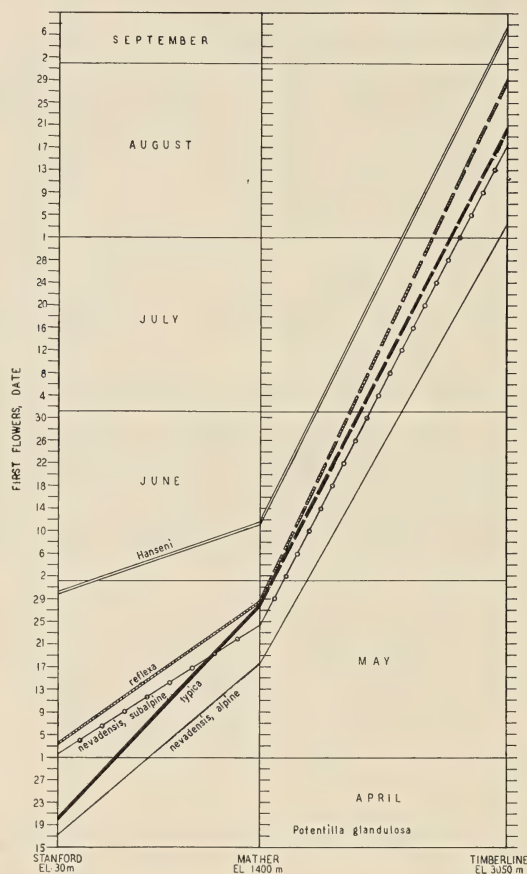


FIG. 36

the basis of latitudinal difference, in the other two subspecies, on the basis of altitudinal differences. Within each of these three subspecies, the races are only moderately distinct as to height at Stanford, but show much greater differences at Mather. This brings out a point that has been noted several times: ecotypical differences may

be accentuated at one station over another, and the most vivid impressions of these differences are obtained at that garden where the species as a whole does its best.

It should be noted that in both *reflexa* and *typica*, one race grows tallest at Mather, while the other race grows tallest at Stanford. This aberrant behavior possibly indicates that additional ecotypes are under differentiation in each of these subspecies.

The broken lines in this figure and the next indicate that the ecotypes so marked do not survive well at Timberline, and consequently the data for that station are scanty. Both of these figures are drawn from three-year averages of many individuals.

The date on which first flowers appear in the various ecotypes at the three stations is shown graphically in figure 36. In this figure the groups of ssp. *typica* and ssp. *reflexa* which were separated in figure 35 have been united, because they showed no significant difference in earliness. It is of interest that in a subspecies such as *reflexa*, in which the highest and lowest elements are separated by 1500 m. in altitude, all flower at approximately the same time at any one of the three stations, regardless of the elevation of the original habitat.

Tables 10 and 11 give a condensed review of the differences between the ecotypes of *Potentilla glandulosa* at the various stations. Table 10 gives the differences in plant height at Mather, and table 11 the differences in earliness (dates of first flowers) at all three stations. It will be noted that all the ecotypes are significantly different from one another in earliness, if not at one station, then at another.

A comparison of the behavior of these ecotypes in the water-light gardens at Mather is given by graphs in figures 37 to 39. The points on these graphs represent the means of the four-year averages for many individuals. In figure 37 the heights of plants are plotted. No two ecotypes follow similar patterns in these gardens. The mean height of plants of ssp. *reflexa* is essentially the same under the four sets of conditions. Ssp. *Hanseni* and the two ecotypes of ssp. *nevadensis* have the shortest stems in the dry shade garden. They are sun-loving meadow plants. Ssp. *typica* and its probable derivative, ssp. *globosa*, are shortest under dry sun conditions, owing in part to their elongation in response to shade.

In figure 38 the number of stems produced under the four sets of conditions in the water-light gardens is shown. This represents a

TABLE 10
DIFFERENCES IN HEIGHT BETWEEN ECOTYPES OF *POTENTILLA GLANDULOSA* AT MATHER (IN CM.)

Ecotypes		Ssp. <i>nevadensis</i>		Meadow ecotype, ssp. <i>Hanseni</i>	Ssp. <i>reflexa</i>		Ssp. <i>typica</i> from Oregon
		Alpine	Subalpine		High altitude	Low altitude	
Coast Range ecotype, ssp. <i>typica</i>	From California	+9.92 ± 4.82 <i>t</i> = 2.059 (44)	+31.68 ± 4.53 <i>t</i> = 6.996 (39)	+52.72 ± 7.19 <i>t</i> = 7.332 (18)	+3.46 ± 4.17 <i>t</i> = 0.830 (25)	+36.73 ± 4.61 <i>t</i> = 7.967 (30)	+21.40 ± 7.59 <i>t</i> = 2.819 (18)
	From Oregon	-11.48 ± 7.00 <i>t</i> = 1.640 (36)	+10.28 ± 7.41 <i>t</i> = 1.388 (31)	+31.32 ± 9.28 <i>t</i> = 3.375 (10)	-17.94 ± 7.18 <i>t</i> = 2.499 (17)	+15.53 ± 7.81 <i>t</i> = 1.988 (22)	
Foothill ecotype, ssp. <i>reflexa</i>	Low altitude	-27.01 ± 3.56 <i>t</i> = 7.598 (48)	-5.25 ± 4.30 <i>t</i> = 1.221 (43)	+15.79 ± 7.05 <i>t</i> = 2.240 (22)	-33.47 ± 3.90 <i>t</i> = 8.584 (19)		
	High altitude	-6.46 ± 2.93 <i>t</i> = 2.203 (43)	+28.22 ± 3.80 <i>t</i> = 7.424 (38)	+49.26 ± 6.76 <i>t</i> = 7.287 (17)			
Meadow ecotype, ssp. <i>Hanseni</i>		-42.80 ± 6.57 <i>t</i> = 6.519 (36)	-21.04 ± 6.99 <i>t</i> = 3.007 (31)				
Subalpine ecotype, ssp. <i>nevadensis</i>		-21.76 ± 3.45 <i>t</i> = 6.305 (57)					

t = — mean difference
 — standard error

Boldface type indicates statistically significant differences (*t* value greater than the 5 % level). The figures in parentheses indicate the total number of plants in the two groups compared. The differences have been obtained by subtracting values of the ecotypes at the left from those of the ecotypes above.

TABLE 11
DIFFERENCES IN EARLINESS BETWEEN ECOTYPES OF POTENTILLA GLANDULOSA
AT THREE STATIONS (IN DAYS)

Ecotypes	Station	Ssp. nevadensis		Meadow ecotype, ssp. Hanseni	Ssp. reflexa
		Alpine	Subalpine		
Coast Range ecotype, ssp. typica	Stanford	-2.75±2.36 t = 1.168 (38)	+11.51±2.40 t = 4.803 (38)	+39.30±4.16 t = 9.447 (20)	+12.16±2.14 t = 5.677 (62)
	Mather	-10.71±0.97 t = 11.064 (48)	-3.66±0.94 t = 3.877 (44)	+14.72±1.85 t = 7.957 (23)	+0.64±0.91 t = 0.703 (65)
	Timberline	-16.47±9.18 t = 1.795 (31)	-2.33±9.34 t = 0.249 (23)	+19.00±10.31 t = 1.843 (9)	+9.30±9.65 t = 0.964 (19)
Foothill ecotype, ssp. reflexa	Stanford	-14.91±1.64 t = 9.097 (70)	-0.65±1.70 t = 0.383 (70)	+27.14±4.78 t = 5.680 (52)	
	Mather	-11.35±0.78 t = 14.533 (77)	-4.30±0.75 t = 5.726 (73)	+14.08±1.76 t = 8.000 (52)	
	Timberline	-25.77±3.21 t = 8.036 (44)	-11.63±3.66 t = 3.180 (36)	+9.70±5.68 t = 1.708 (22)	
Meadow ecotype, ssp. Hanseni	Stanford	-42.05±3.92 t = 10.727 (28)	-27.79±3.94 t = 7.046 (28)		
	Mather	-25.43±1.79 t = 14.183 (35)	-18.38±1.78 t = 10.326 (31)		
	Timberline	-35.47±4.83 t = 7.344 (34)	-21.33±5.14 t = 4.150 (26)		
Subalpine ecotype, ssp. nevadensis	Stanford	-14.26±1.96 t = 7.279 (46)			
	Mather	-7.05±0.82 t = 8.587 (56)			
	Timberline	-14.14±2.11 t = 6.714 (48)			

See explanation to table 10.

more accurate measure of vigor than stem height, for height increases may often be accompanied by attenuation of the parts and actual decrease in vigor. This figure, in contrast to the preceding, shows all the ecotypes roughly following a common pattern of reaction, with the most stems produced in the moist sun plot and the fewest produced in the dry shade. The greatest fluctuation in this

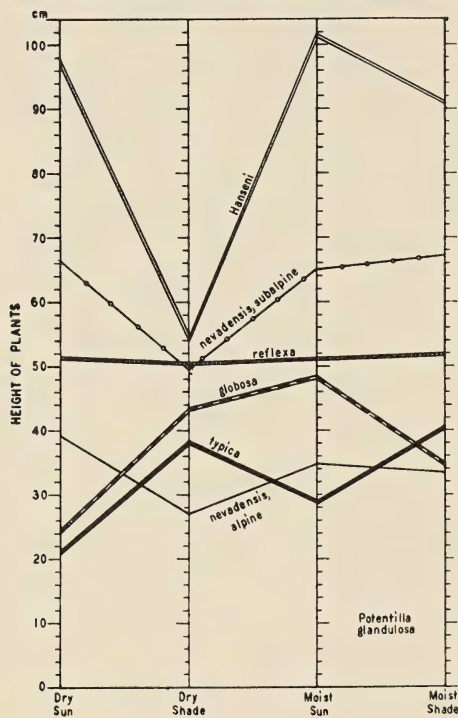


FIG. 37

Modifications in height (fig. 37) and number of stems (fig. 38) in clones representing various ecotypes of *Potentilla glandulosa* in the water-light gardens at Mather.

The graphs are constructed for the plants listed in table 9 from data averaged for the years 1934 to 1937.

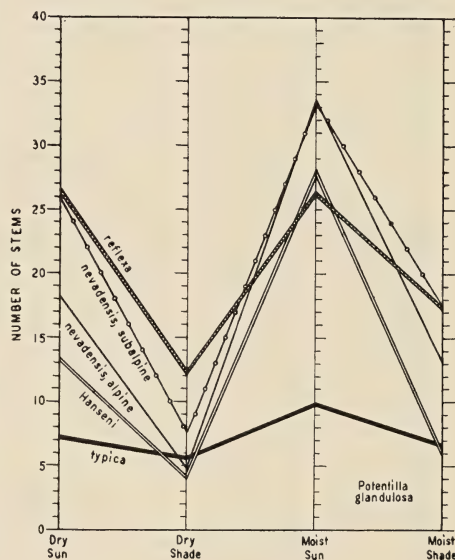


FIG. 38

character is shown by *nevadensis*, while the greatest stability is maintained by *typica*, which is at the other altitudinal extreme in its original habitat and commonly found growing in the shade of trees.

The date when first flowers appear under water-light variation is presented in figure 39. Except for a slight delay in moist shade, these local environmental differences have very little effect on the flowering time. The variation between the ecotypes is greater than the variation within one ecotype under four environments. The

relative positions of the ecotypes in respect to this feature are the same in the water-light gardens at Mather as they are in the interstation garden there as shown in figure 36. Ssp. *Hanseni* blooms considerably later than the others under all conditions, and the alpine ecotype of ssp. *nevadensis* is consistently the first one in flower, while the four other ecotypes cluster in between. It is notable that the difference between the morphologically indistinguishable alpine and subalpine ecotypes of *nevadensis* is far greater than the differences between the morphologically distinct subspecies *typica*, *globosa*, *reflexa*, and *nevadensis* subalpine.

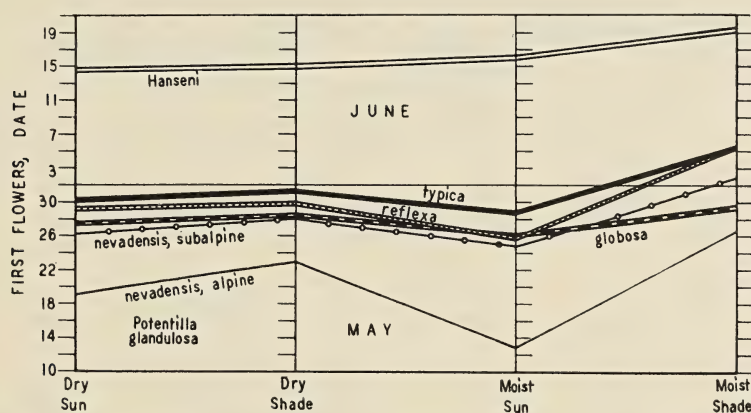


FIG. 39. Modifications in dates of first flowers in clones representing various ecotypes of *Potentilla glandulosa* in the water-light gardens at Mather.

The graphs are constructed for the plants listed in table 9 from data averaged for the years 1935 and 1936.

DIFFERENTIAL SURVIVAL, FLOWERING, AND RIPENING OF THE ECOTYPES. The survival at the three transplant stations of individual clones of the ecotypes discussed on the preceding pages is charted in figures 40 to 42. In comparing the three figures, one may observe that all ecotypes survive successfully at Mather. The record at Stanford is also quite good, except that the survival of alpine *nevadensis* is irregular, and that some individuals have a tendency to omit flowering. The greatest differences between ecotypes are seen at Timberline, where only the alpine is really successful. The almost complete failure of ssp. *typica* and *reflexa* to survive there is marked. Plants of *reflexa* from Upper Tuolumne Canyon, some of which came from 2070 m. elevation, live no better there than those from eleva-

tions not much over 900 m. The subalpine ecotype survives almost as well at Timberline as the alpine, but many plants flower and then fail to ripen their seed. This is especially obvious in years with

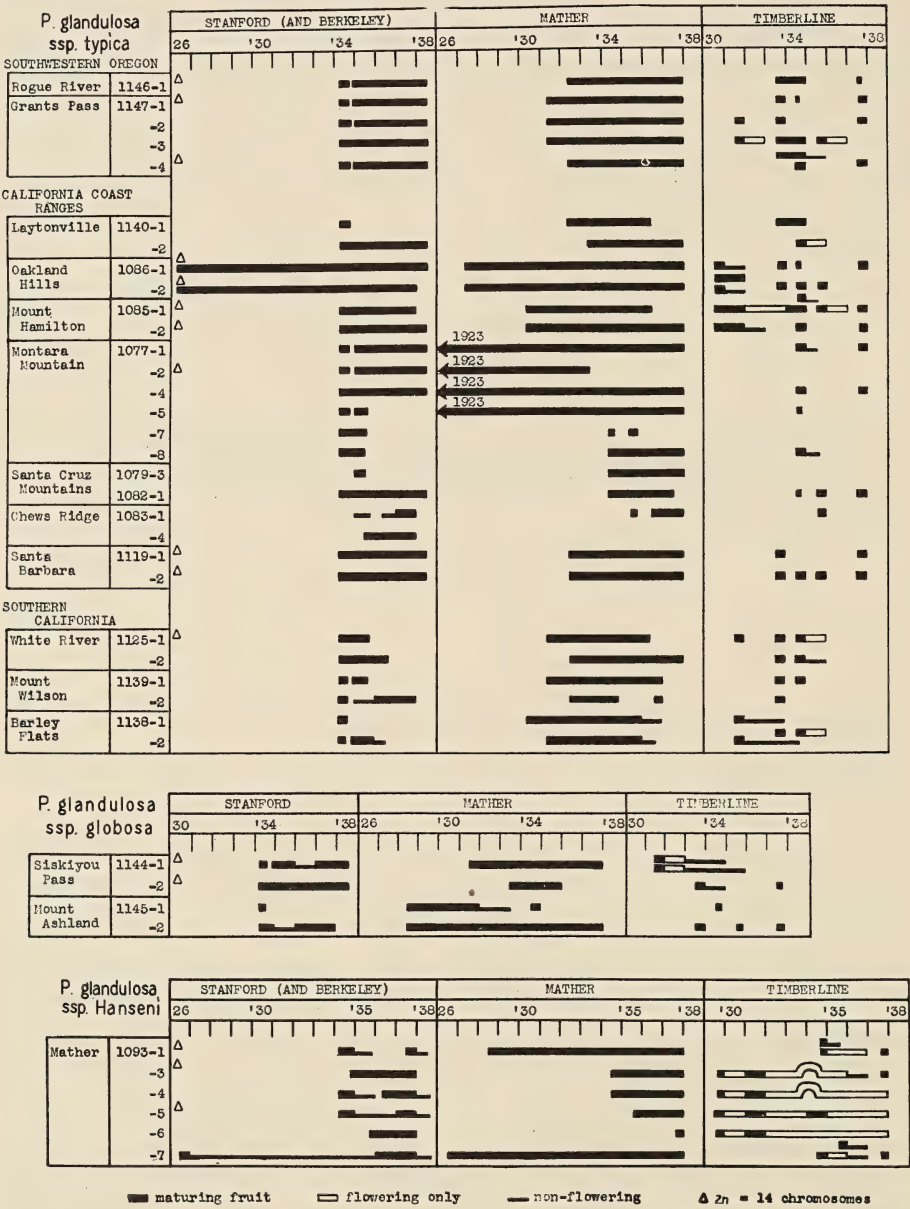


FIG. 40. Record of survival and flowering of clones of *Potentilla glandulosa* at three altitudes: subspecies *typica*, *globosa*, and *Hansenii*. The scale indicates years.

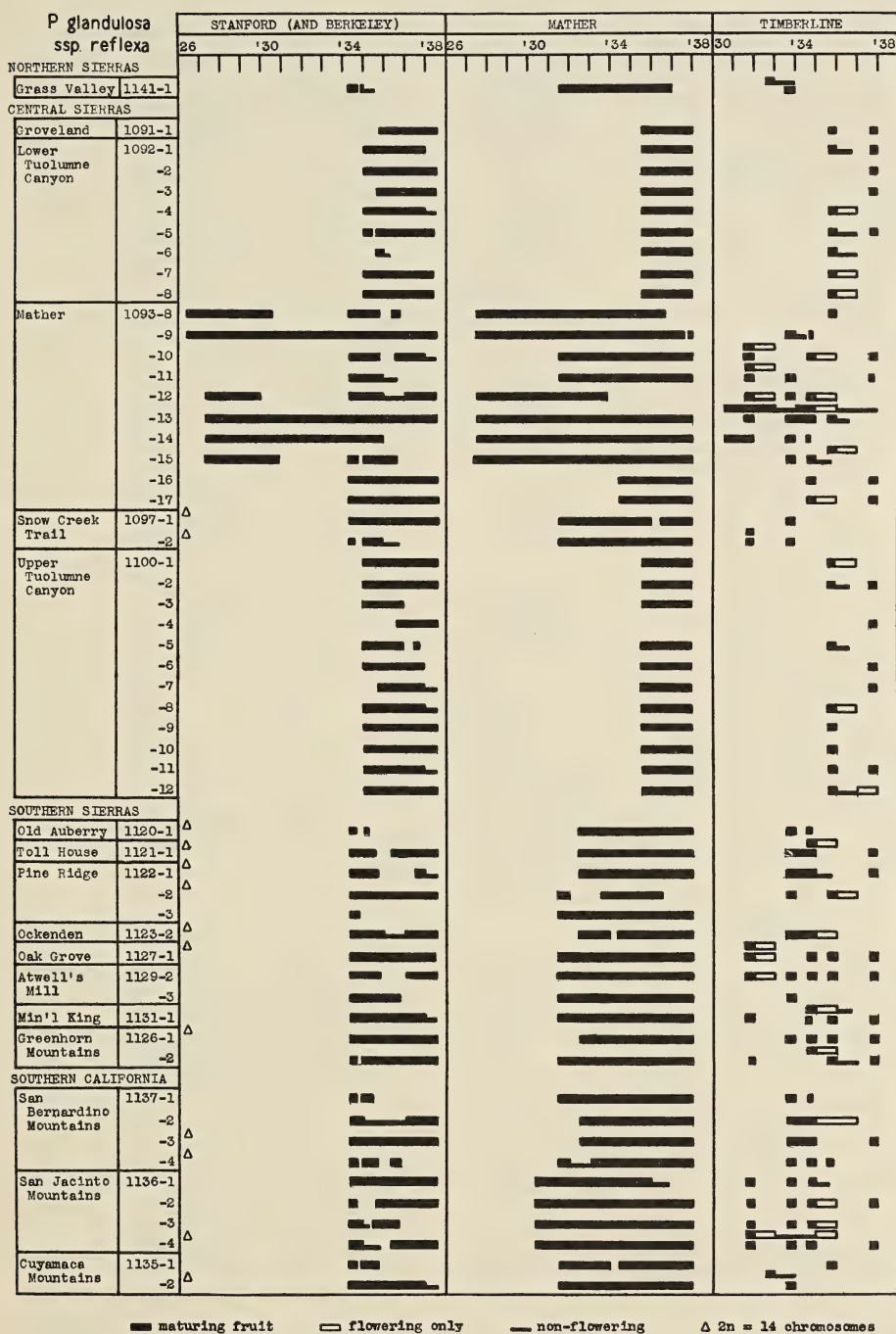


FIG. 41. Record of survival and flowering of clones of the foothill ecotype, *Potentilla glandulosa* ssp. *reflexa*, at three altitudes. The scale indicates years.

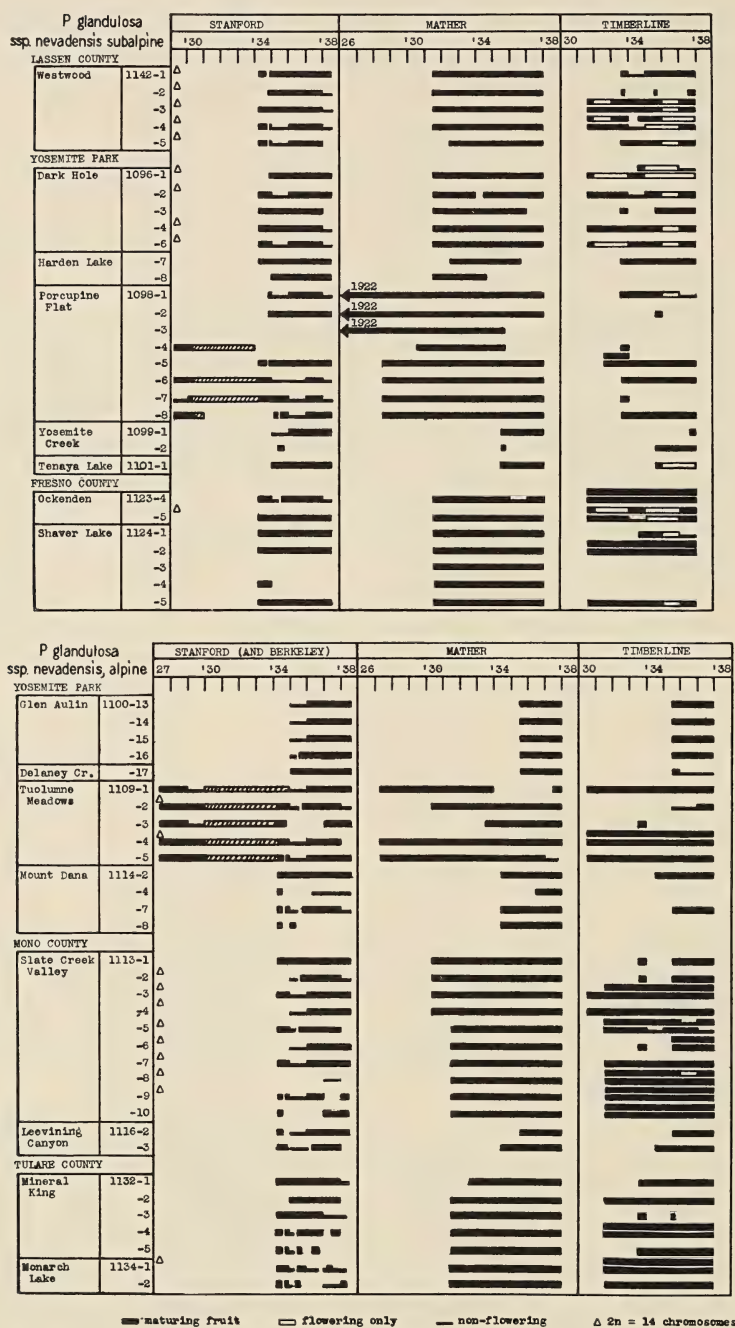


FIG. 42. Record of survival and flowering of clones of subalpine and alpine ecotypes of *Potentilla glandulosa* *ssp. nevadensis* at three altitudes. The scale indicates years. Shaded line indicates that the plant was kept in a lathhouse at Stanford.

retarded seasons, as for example in 1936, when a much larger proportion of the plants of this ecotype failed to mature seed.

Subspecies *Hanseni* is unusual because of its relatively successful survival at Timberline and its persistent flowering each year, but only in the exceptionally early year 1931 did it have much success in ripening fruit. The two curves in the lines of this subspecies indicate that during the winter 1933-1934 those two plants were held at the Stanford nursery for propagation.

The inability of the lowland forms to survive at Timberline appears to be linked to an inability to synthesize enough carbohydrates and other food materials during the short growing season to carry them through the winter. Progressive weakening year by year at Timberline of many transplants from various families points to this factor as a probable cause.

DEVELOPMENT OF ANTHOCYANIN. Almost all the individuals of *ssp. reflexa* develop anthocyanous pigment in their herbaceous parts at all three stations, but there is a difference in the degree of pigmentation developed, depending upon the garden in which the plants are growing. The color is observed to be most intense at Timberline. The individuals of *ssp. nevadensis* develop scarcely any pigment at Mather and Stanford, yet a coloring develops on the stems, petioles, and leaf veins of these plants at Timberline. At Stanford and Mather the only traces of anthocyanin are confined to the basal portions of the stems, which are concealed by the leaf sheaths. This pigment is usually deepest in springtime. At the alpine station the red color becomes evident especially during cold summers with frosty nights.

The presence or absence of anthocyanin in these *Potentillas*, therefore, is primarily a constant character governed by inheritance, which may differ from ecotype to ecotype as shown; but the quantity produced may be influenced by the environment. The increased coloration of plant parts due to anthocyanin at high as compared with low altitudes has also been observed by Kerner (1891) and Bonnier (1895).

RESISTANCE TO COLD. The various races of *Potentilla glandulosa* behave differently with respect to their resistance to cold. At Stanford, races from the Coast Ranges are distinctly less dormant than the mid-Sierran, subalpine, and alpine forms. The mild frosts that

occur at this low altitude during December and January invariably induce nearly complete dormancy in the Sierran forms, especially the alpine races, but do not seriously curtail growth in plants native to the coast region. Moreover, we have repeatedly observed that early fall frosts at Mather and Timberline damage the foliage of subalpine and alpine forms more than that of Coast Range forms. The leaves of coastal forms are actually the most frost-resistant. This situation, which on first sight appears anomalous, is perhaps connected with the fact that the coastal forms are in active growth in their native environs during the cold season at the time of most rainfall, while the alpine forms in theirs grow during the summer only and are dormant through the long, severe winter. The coastal forms are not able to survive at Timberline, however, which indicates that survival in alpine climates, in this instance at least, has nothing to do with cold resistance of herbage.

CYTOGENETIC STUDIES

OBJECTIVES. The purpose of this phase of the investigations on the *Potentilla glandulosa* complex was to interpret the taxonomic status of the various forms by testing the degrees of genetic relationship, to explore their evolutionary background by analysis of gene or chromosome differences, and to determine their utility for various ecogenetic investigations.

It was early realized that the low and uniform chromosome number, in connection with the marked ecologic differentiation, would make *Potentilla glandulosa* a choice subject for combined genetic and ecologic investigations, provided the ecologic units were ecotypes rather than ecospecies. If they were ecotypes, they could be crossed and would produce a second generation in which the parental genes would be recombined in all proportions without resulting constitutional weakness in the offspring. If, however, they belonged to different ecospecies, the genic recombinations in the hybrids would produce many constitutionally weak offspring (see *Zauschneria*, p. 254), which would barely survive even under the favored conditions of the experiment field. Crosses between ecospecies, then, would be useless for testing the results of exchanging and recombining genes that determine the fitness of plants for their environments. The results would be obscured by the presence of two kinds of unfitness; one,

constitutional weakness due to unbalanced interreaction of the genes among themselves, and the other, environmental unfitness.

CYTOLOGY. It was previously mentioned (p. 30) that all forms of *Potentilla glandulosa*, as well as all other species investigated of the section *Drymocallis*, are diploid ($n=7$). This is an interesting example of cytological uniformity within a species complex of holarctic distribution, and of an ecological differentiation that permits its members to fit exceedingly different environments. It follows that the diversity distinguishing ecotypes and ecospecies has been produced by simple genic differentiation. It was also mentioned that Popoff (1935) found the hybrid between the Eurasiatic *P. rupestris* and *P. geoides* to be very fertile. He produced forty-two F_1 plants and found the chromosomes conjugating completely in the hybrid. Accordingly, these morphologically quite distinct units have very homologous chromosomes, and their genic incompatibility, if any, is slight.

EVIDENCE OF SELF-FERTILITY AND SELF-INCOMPATIBILITY; INBREEDING. Some ecotypes of *Potentilla glandulosa* are self-fertile, such as ssp. *typica* and *reflexa*, which have small, relatively inconspicuous flowers. Others are self-incompatible, such as the forms of ssp. *nevadensis*, which have large, attractive flowers.

Constancy of the ecotypes has been tested very little. One selfed culture of ssp. *reflexa* from Oak Grove (1127-1), consisting of seventy plants, was grown. These plants were very uniform in all respects, closely resembling their foothill parent. Self-pollinations were attempted on the alpine ecotype also, but the akenes obtained were very few and mostly shriveled. From two self-pollinations in different years only two very weak offspring were obtained from a plant native at Timberline station (1113-6). The high alpine 1134-1, from Upper Monarch Lake, at 3240 m. elevation, was also tested, but no offspring were obtained. A large sample of many forms of *P. glandulosa* was tested for self-fertility in an insect-proof greenhouse, but those mentioned were the only plants from which selfed seed were sown.

Seedlings of *P. glandulosa* require two years to reach maturity, for only a rosette is developed the first year. Since four years are necessary to obtain a second generation, plants of this section of *Potentilla*

are less suited to genetic investigation than other species. Their great advantage lies in their suitability for ecogenetical studies.

CROSSINGS. Hybrids between the Coast Range, the foothill, and the alpine ecotypes have been produced in a preliminary survey of the taxonomic status of the subunits under *P. glandulosa*. They are illustrated between their parents in figure 43 as they appear when grown in the Stanford garden. It can be seen that the two alpine plants are very dwarf there, especially 1134-1 from Monarch Lake. This plant, incidentally, flowered only once in the Stanford garden. The closely aggregated flowers in *typica* and in 3299, its hybrid with *nevadensis*, are also shown. The flexuous divaricate branching characteristic of *reflexa* is evident in both its hybrids.

Other differences between these forms, some of them listed in table 1 in the taxonomic part of this chapter, do not show in the photograph. Only one F_2 generation has been grown, namely, one from selfing the hybrid illustrated by 1442-1.

The hybrids produced between ecotypes of *Potentilla glandulosa* are listed below:

Ssp. *typica* \times ssp. *reflexa*:

- (1) 1119-1, Santa Barbara \times 1127-1, Oak Grove, and reciprocal:

F_1 (3298) consists of 111 plants, all very vigorous and quite uniform. F_1 is glandular-pubescent and anthocyanous and has yellowish-white petals, shorter than the sepals, like both parents. The very fertile F_1 would probably be classified as a *typica* with a moderately open inflorescence if a plant of that appearance were encountered in nature. As in *typica*, the very coarse leaves of this hybrid remain active during the winter. No F_2 has been grown.

Ssp. *typica* \times alpine ecotype of ssp. *nevadensis*:

- (2) 1119-1, Santa Barbara \times 1134-1, Upper Monarch Lake, and reciprocal:

The two parents come from the most extreme habitats occupied by any *P. glandulosa*, namely, the immediate vicinity of the Pacific and 3240 m. elevation in the Sierra Nevada. F_1 (3299) consists of 56 plants with slightly shorter stems than the preceding hybrid, and large white petals (longer than sepals), thin leaves, sparsely pubescent herbage, and a congested, somewhat glandular inflorescence. Unlike the preceding hybrid, this is dormant at Stanford for a short period during the winter, but it starts activity much earlier than the alpine parent. Although one parent is strictly self-incompatible, this hybrid is at least 50 per cent self-fertile. No F_2 has been grown.



FIG. 43. Subspecies of *Potentilla glandulosa* and their F₁ hybrids; specimens taken from plants grown at Stanford.

Ssp. *reflexa* \times alpine ecotype of ssp. *nevadensis*:

- (3) 1127-1, Oak Grove \times 1134-1, Monarch Lake; the reciprocal not produced: F_1 (1441) consisted of 13 plants, rather similar to the subalpine ecotype in height and foliage and in having large creamy-white petals, but the stems were anthocyanous. They are rather highly self-fertile. F_1 has been transplanted to the mountain stations and survives fairly well at Timberline, as will be seen in more detail below. F_2 not grown.
- (4) 1127-1, Oak Grove \times 1113-6, near Timberline station: F_1 (1442-1443) consisted of 11 plants, all rather uniform and similar to the subalpine ecotype, except that the stems are moderately anthocyanous, but it is self-fertile and as early as most members of the alpine ecotype. The F_1 has been tested at the mountain stations, but unlike cross 3 it survives for only one or two winters at Timberline. A total of 670 F_2 plants have been grown; they were all healthy and vigorous, except for 3 per cent, which were weak dwarfs.

The chromosomes conjugate perfectly in these hybrids, as in Popoff's hybrid, *P. rupestris* \times *P. geoides*.

In summary, then, the hybrids between forms from extreme environments of *Potentilla glandulosa* are easily produced, they are fully fertile, the second generation is as vigorous and healthy as the grandparents, and the chromosomes conjugate perfectly. As far as this evidence goes, it means that the regional races are true ecotypes of one large and very variable ecospecies, although undoubtedly they are in an evolutionary process that will finally make some of them distinct ecospecies.

The alpine *nevadensis* and the foothill *reflexa* are morphologically as different as any of the ecotypes of *Potentilla glandulosa*. A list of the most conspicuous differences is given in table 12. From the length of this list, some taxonomists who base their classification on morphologic characters only might insist that the two forms were good species. There are, for example, the very conspicuous differences in the petals, involving length, width, and color; in *reflexa* the petals are shorter and narrower than the sepals, but in *nevadensis* they are nearly twice as long and much wider than the sepals. The seed-coat color is directly correlated with presence or absence of anthocyanin.

More important for survival are the reproductive and physiological differences. The alpine ecotype has a capacity for reproducing by long stolons, but the foothill ecotype has very little vegetative reproduction. The alpine is self-incompatible, while the foothill form is

self-fertile. Their F_1 , being self-fertile and having large, showy petals, breaks the rule otherwise prevailing in *Potentilla glandulosa*. The alpine ecotype has a definite period of dormancy even in the Stanford garden. In the *reflexa* parent this period is much shorter, and in mild winters almost negligible. In spite of this handicap for the alpine parent, it will blossom at Stanford one week earlier than the foothill parent. Both, however, are among the earliest plants of

TABLE 12
DIFFERENCES BETWEEN ALPINE AND FOOTHILL ECOTYPES
OF *POTENTILLA GLANDULOSA* AT STANFORD

CHARACTER	Alpine <i>nevadensis</i> , 1113-6	<i>reflexa</i> , 1127-1
Stolons	Long	Short or none
Habit	Low, 21 cm.	Tall, 46 cm.
	Erect	Divaricate
Pubescence	Glabrate	Densely pilose
	Non-glandular	Glandular
Stem color	Green	Anthocyanous
Earliness	Very early, April 4	Early, April 12
Reproduction	Self-incompatible	Self-fertile
Petals {	Length	Short
	Width	Narrow
	Direction	Reflexed
	Color	Deep yellow
Seeds {	Size	Medium
	Color	Brown

their respective ecotypes, especially the *reflexa* parent, which is about two weeks earlier at Stanford than any of the other plants of the foothill ecotype (see table 5).

REACTIONS OF F_1 HYBRIDS TO DIFFERENT ENVIRONMENTS. The reactions of the F_1 populations are very characteristic. The modifications in plant height and number of stems in clone members at the three transplant stations follow a pattern similar to that found in plants of the subalpine ecotype. The hybrids are as early, however, as the alpiners, except that they are a little delayed at Stanford. These characteristics are obvious from table 13, which lists the reactions of twelve individual plants of crosses 3 and 4. It may be noticed that the F_1 plants of 1127-1 \times 1134-1 (cross 3) are a trifle earlier at Timberline than those of the other cross and its reciprocal.

TABLE 13

POTENTILLA GLANDULOSA SSP. NEVADENSIS \times SSP. REFLEXA, F₁: MODIFICATIONS IN VIGOR AND EARLINESS
(Averages from 1935 to 1937, except that at Timberline data were available usually from one year only)

PLANT NUMBER	HEIGHT OF PLANTS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
1127-1 × 1134-1:									
1441-1.....	37.6	63.0	28.5	12.0	25.0	5.5	Apr. 27	May 15	Jul. 31
-2.....	42.6	67.0	27.5	20.0	32.5	3.0	Apr. 16	May 23	Jul. 31
-3.....	25.0	64.6	26	3.0	23.0	3	Apr. 25	May 14	Aug. 1
-4.....	31.6	57.0	24	2.5	24.0	5	Apr. 23	May 15	Jul. 30
-5.....	62.3	25.7	21.3	8.0	May 13	Jul. 29
-6.....	36.0	63.3	19.0	24.7	Apr. 29	May 14
1127-1 × 1113-1:									
1442-1.....	47.6	60.5	30	22.0	22.5	15	Apr. 18	May 17	Aug. 1
-2.....	43.0	59.3	20	22.0	26.7	1	Apr. 27	May 21	Aug. 12
-3.....	33.3	65.7	22	9.0	29.3	3	Apr. 22	May 17	Aug. 4
1113-1 × 1127-1:									
1443-1.....	39.3	61.3	30	19.0	27.0	6	Apr. 28	May 20	Aug. 6
-2.....	45.0	57.5	24.0	30.0	Apr. 21	May 17
-3.....	38.7	30	25.3	2	Apr. 13	Aug. 6
Means.....	38.1	62.0 ±0.94	26.4	16.2	26.0	5.2	Apr. 22.7 ±1.57	May 16.7 ±0.93	Aug. 2.4 ±1.37
Mean dif- ferences. t =		Ma-St:23.5 ± 2.66; 8.835 Ma-Ti:36.3 ± 1.65 22.000		Ma-St:11.2 ± 2.05; 5.463 Ma-Ti:21.1 ± 2.39 8.828			Ma-St:24.0 days; Ma-Ti:24.0 days		Ti-Ma:77.7 days

POTENTILLA GLANDULOSA SSP. NEVADENSIS \times SSP. REFLEXA: COMPARISON BETWEEN HYBRID AND PARENTS

TABLE 14

CHARACTER	FOOTHILL PARENT, 1127-1			HYBRID F1: 1442-1443 (AVERAGES OF 6 PLANTS)			ALPINE PARENT, 1113-6		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
Height (cm.).....	45.7	69.7	(6)	41.1	60.9	26.4	20.5	42.3	34.0
No. flowering stems.....	25.0	62.5	(1)	26.2	23.0	9.0	27.5	27.5	13.5
Date of first flowers.....	Apr. 12	May 22	Aug. 26	Apr. 21	May 18	Aug. 6	Apr. 4	May 14	Jul. 30
Survival at Timberline.....	None	1-2 years	Excellent

The standard errors for the combined hybrid populations are small as compared with samples of *Potentilla* from natural habitats in previous tables, although there are only twelve F_1 individuals. This means that the F_1 's are more uniform than most wild populations, which would be expected from the fact that genes of only three individuals entered the two hybrids.

For a comparison between *nevadensis*, Timberline \times *reflexa*, Oak Grove (cross 4) and its parents, turn to table 14 and figures 44 and 45. The F_1 is somewhat intermediate between its parents in height at Stanford and Mather, although it is much closer to *reflexa* than to alpine *nevadensis*. But at Timberline the height of F_1 is conspicuously decreased to even below that of its alpine parent. This is possibly correlated with the fact that F_1 does poorly there. Also the *reflexa* parent was modified to extreme dwarfness the only year it managed to survive and flower on the Timberline slope; its single flowering stem was only 6 cm. long (table 14). Accordingly, even at Timberline the F_1 is "intermediate," although heights of the parents are reversed here. The hybrid is also intermediate as to survival at Timberline. The alpine parent survives indefinitely, whereas the foothill parent is the one most consistently eliminated at Timberline of all the races of its ecotype. The hybrid survives for few years only.

A comparison of earliness between the parents and the hybrid is presented graphically in figure 45. The parents flower on the average just one week apart at both Stanford and Mather, but the behavior of the hybrid is unpredictable. It is intermediate between its parents at Mather, but is one week later than the *reflexa* parent and two weeks later than the *nevadensis* parent at Stanford. As yet we have no satisfactory explanation for this phenomenon, except that it tells us that the interreactions of the factors that determine the time of flowering of a plant in a certain environment are very complex indeed. There may be interference between the activity of groups of genes that determine the period of dormancy, and that of other groups of genes that determine speed of growth. At any rate it is an interesting situation that becomes of greater significance when we observe what happens in F_2 .

RECOMBINATIONS OF THE GENES DISTINGUISHING THE ECOTYPES. The second generation of this hybrid between an alpine and a foothill ecotype presents a picture of the variation commonly seen in the F_2

of hybrids between ecotypes of one ecospecies. Here we observe the effects of recombinations of the genes which determine the long list of characters that distinguish one parent from the other (see table 12). Each of these fourteen characters shows segregation, both the

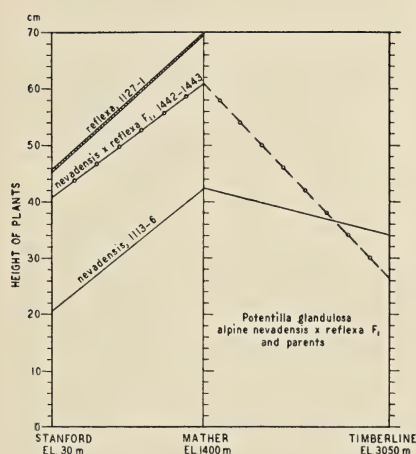


FIG. 44

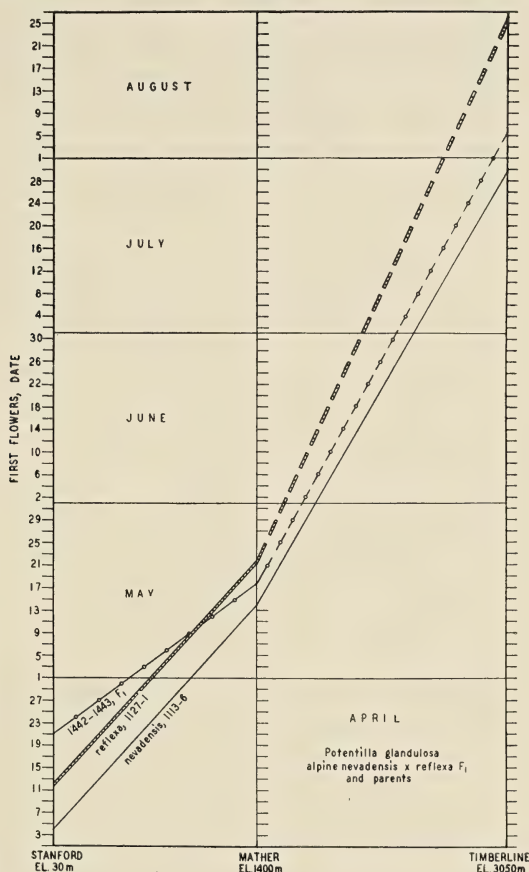


FIG. 45

Modifications in heights (fig. 44) and dates of first flowers (fig. 45) of six clones of alpine *nevadensis* \times *reflexa* F_1 and their parents at three altitudes.

Data averaged from the years 1935 to 1937. Broken lines between Mather and Timberline indicate failure of prolonged survival at the alpine station.

morphologic and the physiologic ones. None of them appears to be due to a single gene difference. Classification was attempted for earliness, relative length and width of petals, color of petals, height of plants, and presence or absence of anthocyanin; all these characters appeared to involve complex combinations of genes. With only seven pairs of chromosomes, and with gene differences certainly

exceeding this number many times, much linkage should be expected unless the percentage of crossing-over is generally high.

The petals showed great variation in size among the 544 F_2 individuals classified. At one extreme there were plants with petals smaller than the sepals, like *reflexa*; at the other, there were plants with petals larger than the sepals, like *nevadensis*. A transition from one extreme to the other is found in the intermediates; the extremes exceeded both parents with respect to size of petals. Large-petaled forms were most numerous, as would be expected from the appearance of the F_1 . Similarly, the color of the petals varied from the

TABLE 15

POTENTILLA GLANDULOSA, ALPINE NEVADENSIS \times REFLEXA F_2 : CORRELATION
BETWEEN COLOR AND SIZE OF PETALS AT STANFORD

Petal size \ Petal color	Petal color			Total
	White	\pm Cream	Yellow	
Large.....	71	229	5	305 (11 extra large)
Intermediate.....	8	102	61	171
Small.....	1	20	47	68 (3 extra small)
Total.....	80	351	113	544

whitish of the *nevadensis* parent, through intergrades to the deep yellow of the *reflexa* parent. The segregations for petal size and petal color are given in table 15, with the many variations under each classified into three groups.

Special interest was attached to the classification of earliness, because this character is closely correlated with the ability to survive in certain environments. The results of a tabulation made at Stanford during the first year the culture flowered were unexpected. As shown in table 16, some plants came into flower about March 20, others not until early June. Some were earlier than the alpine parent, and even earlier than any other plants of *Potentilla glandulosa* in the transplant experiments; others were extra late, and some did not produce flowers during the year in which the tabulations were taken (1937). The latter may have been either extra late, or forms that have to an extreme degree the characteristic alpine tendency of failing to flower at Stanford, as for example 1134-1 from Upper Mon-

arch Lake, illustrated in figure 43. The great majority of F_2 plants grouped themselves between these extremes; some were like their parents in earliness, and others corresponded to the more common forms of *reflexa* and the subalpine ecotype of *nevadensis*.

From this simple analysis it is obvious that all the variation in earliness found in natural populations—and possibly even more—can be produced by recombinations of the genes in a single cross. The transgressive segregation, shown by the presence of plants that are earlier or later than either parent, indicates that earliness is deter-

TABLE 16

POTENTILLA GLANDULOSA, ALPINE NEVADENSIS \times REFLEXA F_2 : CORRELATION
BETWEEN PETAL COLOR AND EARLINESS AT STANFORD

Date of first flowers	Petal color			Total
	White	\pm Cream	Yellow	
March 20–31.....	8	17	1	26 (extra early)
April 1–8.....	42	117	22	181
April 9–19.....	27	139	53	119
April 20–May 31.....	3	78	37	118, subalpine and <i>reflexa</i>
Not yet flowering June 1.....				(17) (extra late)
Total.....	80	351	113	544

mined by many genes located in different chromosomes, or at least at different loci.

It is significant that genetic linkage is shown between the most conspicuous character combinations that serve as key characters for the parent ecotypes. This is evident in the relation of petal size to petal color and in the relation of petal color to earliness (see tables 15 and 16). The latter represents linkage between a morphologic and a physiologic character complex. We have repeatedly found such linkage relations between taxonomically important morphologic characters and those physiologic characteristics important for the survival of the ecotype or ecospecies in its native environment. This may be one reason why ecotypes of one ecospecies remain relatively pure at their points of contact. It also lends added importance to the often discredited morphologic characters. When such correlations have been established by experiment, they become important

key indicators that can be used in tracing the distribution of physiologically important ecotypes.

The genes of two climatically very different ecotypes have reassorted themselves in this hybrid swarm obtained from the cross between the alpine and the foothill ecotype. Close study of the individual reactions of the F_2 plants at all three altitudinal stations becomes therefore important. This study is under way to determine whether adaptation can be produced by genic reassortment and selection, and whether such adaptation results in types morphologically similar to the natives already around the three stations. Because of genetic linkage, this is possibly to be expected.

Potentilla glandulosa presents a picture of evolutionary differentiation into ecologic units, the ecotypes, which are not separated from each other by breeding barriers. The ecotypes fit their specific climates and differ by many characters, both physiological and morphological. Each of these characters appears to be determined by a series of genes, and is often genetically linked with others. The many differences in genes with minute effect furnish the basis for the multiplicity of intergrading forms observed in nature, and the linkage relations suggest a reason for the limited number of taxonomic units that can be recognized in spite of recombinations and lack of internal barriers.

III

POTENTILLA GRACILIS AND ITS ALLIES

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GENERAL RELATIONSHIPS

While *Potentilla gracilis* offers problems in many respects similar to those found in *P. glandulosa*, it presents an opposite picture in other ways. Both groups are of complex composition, and both have ecotypes showing parallel differentiation. Cytologically the two are extreme opposites. *Potentilla glandulosa* and its allies have but one simple chromosome number throughout their entire range covering the three continents in the Northern Hemisphere, whereas the *gracilis* complex is exclusively west American and highly polyploid, and so variable in chromosome number that differences are common even within single populations.

Potentilla gracilis itself occupies the area from Alaska to southern California, and from the Pacific Coast to the Rocky Mountains (see fig. 48). It is most abundant on the Pacific slope. Eastward it is more scattered in distribution, and is in considerable measure replaced by allied species. These relatives are found exclusively to the east of the Cascadean-Sierran axis (fig. 47). There are five of them: *P. flabelliformis* Lehm. and *P. pectinisecta* Rydb., species roughly of the northern and southern halves of the Great Basin respectively; *P. pulcherrima* Lehm., widely distributed through the Rocky Mountains and adjacent chains from British Columbia to New Mexico; *P. brunnescens* Rydb., rather local in Wyoming and northern Colorado; and, finally, *P. diversifolia* Lehm., found only on the highest mountain peaks, but widely distributed in western America between latitudes 35° and 60° north (fig. 48). Four representatives of this complex are shown in figure 46 as they appear in a uniform garden at Mather.

Both the *glandulosa* complex and the *gracilis* complex are found

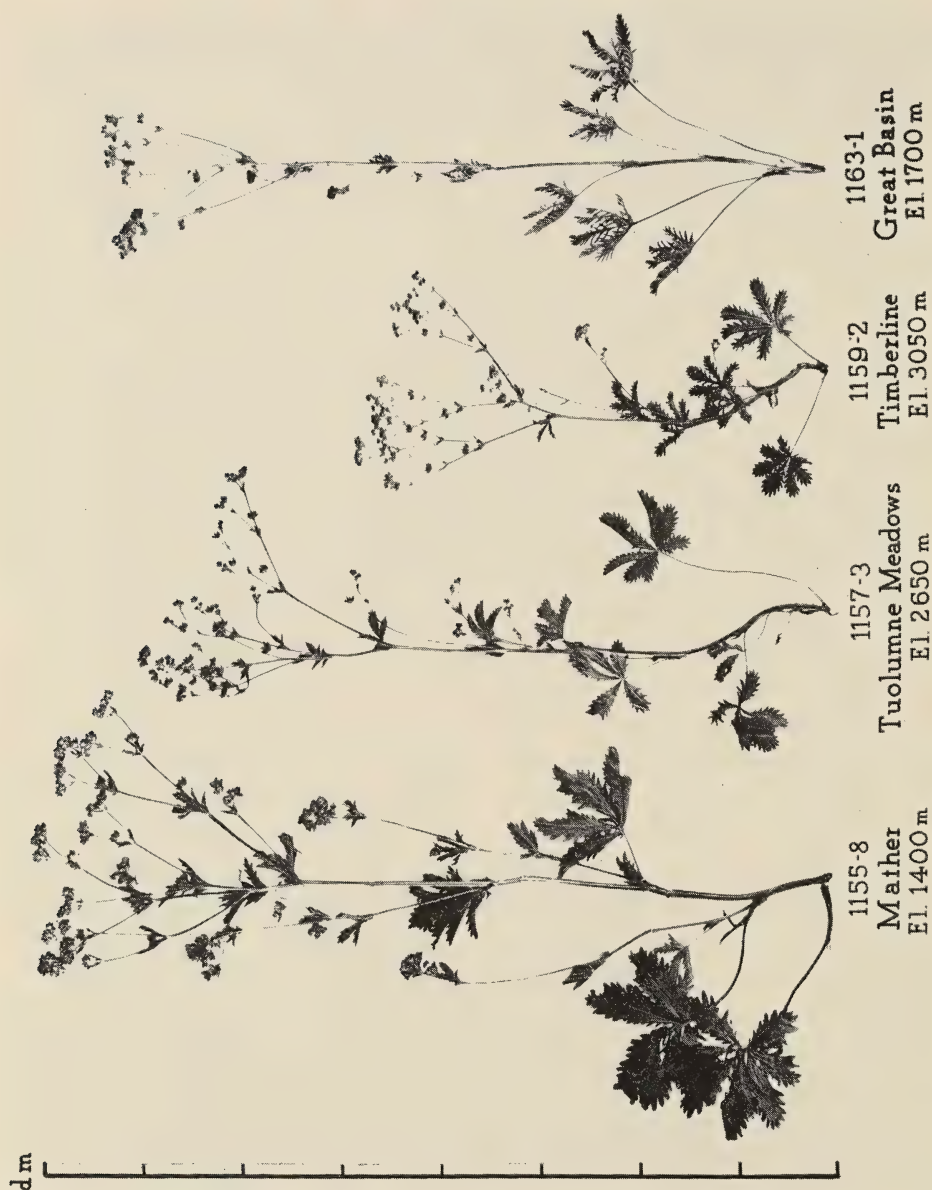


FIG. 46. Races of the *Potentilla gracilis* complex from different altitudes. Specimens from plants growing in a uniform garden at Mather: 1155-8 is from Mather ($2n = \text{ca. } 109$), 1157-3 from Tuolumne Meadows, Yosemite Park, and 1159-2 from near Timberline station ($2n = \text{ca. } 70$); these three are *P. gracilis* ssp. *Nuttallii*. The fourth plant, 1163-1, from Wells, Elko County, Nevada ($2n = \text{ca. } 60-65$), is referable to *P. flabeliformis*.

from sea level to high alpine conditions, with *P. diversifolia*, of the latter group, ascending the highest of all. Several important differences, however, mark the distribution of the two complexes. For instance, *P. gracilis* and its allies have no eastern representative comparable with *P. arguta*. On the other hand, the *glandulosa* complex has not been able to occupy the lower levels in the Great Basin, whereas *P. pectinisecta*, of the *gracilis* group, occupies even the lower subalkaline flats, and forms of *P. gracilis* itself grow in the Upper Sonoran zone of the Great Basin. *Potentilla gracilis*, unlike *P. glandulosa*, is not known from the central portions of the Coast Ranges of California, but it does occur farther north along the immediate coast of Alaska and the Aleutian Islands, which *glandulosa* does not reach.

The cytological situation in *P. gracilis*, *flabelliformis*, *pulcherrima*, and *diversifolia* is characteristic of apomictic species. The chromosome numbers are very high, varying in these four species from $2n \approx 56$ to $2n \approx 109$ —from octoploid to nearly 16-ploid. Almost the full gamut of variation may be found within one species! Indeed, even the individuals of single populations of a species may differ in their chromosome number. Meiosis is very irregular; there may be from 15 to 35 univalent chromosomes, and yet seed production is very good. A fifth species, *P. pectinisecta*, is the only one in which regular meiosis was found. It is hexaploid with 21 bivalent chromosomes, but only two plants from one population were investigated. It is possible, therefore, that even in this species other populations may be discovered that are cytologically as irregular as those of the other species in this complex.

Most of the forms probably reproduce asexually like the European *Potentillas* investigated by Müntzing (1928, 1931), but some sexual reproduction almost certainly takes place in all of these, as indicated by the recombinations of morphological characters to be found in almost any population.

The *gracilis* complex is, therefore, the complete antithesis of the *glandulosa* complex in many respects. In the latter, sexuality and complete cytological constancy prevail, but in the *gracilis* complex there is the highest degree of cytological irregularity and the chromosome numbers are very high. Well-defined ecotypes have evolved even here, however, irrespective of the extreme cytological variation that characterizes even the individual populations.

TAXONOMIC ACCOUNT

A critical study of the group of North American species that are morphologically most closely related to *Potentilla gracilis* Dougl. has been necessary in order to obtain correct names for the various forms we have taken into the transplant experiments. Various monographic treatments of the genus have not succeeded in bringing even an approximately natural order into the North American species, as is evident after even a brief study of the situation. Causes for this result may be suggested: lack of intimate field knowledge of the species; lack of appreciation for the importance of geographic distribution in speciation; lack of sufficient material; failure to consider the rôle of hybridization in nature, which shuffles the morphological characters, and the possibility of apomixis as a factor; dependence upon unit morphological characters for specific criteria, particularly upon the unreliable one of pubescence; and oversight of certain dependable characters in the genus.

As a consequence, the monographic studies of Rydberg (1898, 1908) and Wolf (1908) have failed to place in conjunction species that are the most closely related, as now determined by field and cultural studies. Wolf erred less in this direction than did Rydberg, who depended upon unit morphological characters for the delimitation of species and sections alike. Forms obviously to be included in the same subunit of the species he has often separated by thirty or forty "species" of very different affinity.

The present account does not pretend to be an exhaustive revision of this group. From a study of some nine hundred sheets of herbarium material, and from observations in the field and garden, we conclude that seven groups can be distinguished by their peculiar combinations of morphological characters in conjunction with their natural geographic ranges. For lack of experimental evidence to determine their exact status, we consider that these are best treated at the present time as six species, *P. gracilis*, *flabelliformis*, *pulcherrima*, *pectinisecta*, *brunnescens*, and *diversifolia*. *Potentilla gracilis* is composed of two subspecies. At least one of these is biologically differentiated into regional ecotypes. The synonymy under each tells something of their complexity. The accompanying distribution maps will indicate the naturalness of their ranges.

Of these six species, *P. gracilis* is by far the most complex. Within it one finds an almost bewildering shuffling of the morphological char-

acters even within local populations. Leaf cut, shape of leaflets, size of parts, habit of stems, and abundance and quality of pubescence are among the most variable features. From the variation manifest in single colonies, it seems probable that interbreeding takes place, except when chromosomal barriers intervene; these are considered further below. Since this is the case, we have been led to look for the larger barriers that separate the complex into regional units. The six species as recognized by us might eventually prove to lack genetic barriers for their distinction; but at present they appear to be of about equal rank. Apparent hybrids link *gracilis*, *flabelliformis*, *pulcherrima*, and *pectinisecta*, probably in all possible combinations in localities where they meet, yet these are not sufficiently abundant to warrant treating all as one species. The recombinations that are detected do not mask the distinctness of these four units when much material is examined.

On the other hand, the recombinations between the two subspecies we recognize of *gracilis*, as well as the slight morphological basis for the separation of these units, impel us to consider them as conspecific.

A very few possible hybrid derivatives have been noted between *diversifolia* and *gracilis*. Otherwise *diversifolia* stands out distinctly. *Potentilla brunnescens* is not linked with the others at present through suspected hybrids, but it is of limited distribution and least well known of the six.

KEY TO THE SPECIES AND SUBSPECIES OF GRACILES

- A. Anthers ovate to lance-cordate, mostly 1 mm. long.
- B. Leaflets divided two-thirds of the way or more to the midrib with linear segments, always digitate.
- C. Leaves glandular, with tawny pilose spreading pubescence, not at all tomentose or silky.
Central Rocky Mountains.....1. *P. brunnescens*
- CC. Leaves not glandular or tawny pubescent.
- D. Leaflets strongly discolored, densely tomentose beneath, dark green above, if sericeous, only so along the veins, the teeth not pectinately crowded but spreading. Northern Great Basin to Alberta.....2. *P. flabelliformis*
- DD. Leaflets scarcely discolored, densely silky and beneath often \pm tomentose, gray-

- green, pectinately toothed. Southern Great Basin 3. *P. pectinisecta*
- BB. Leaflets merely crenate or serrate, or if toothed half-way to the midrib the segments broader and less crowded; pubescence various.
- E. Leaves prominently discolored, green above, white-tomentose beneath.
- F. Leaflets shallowly and obtusely serrate, broadly oblanceolate or obovate, digitate or sometimes subpinnate. Rocky Mountains 4. *P. pulcherrima*
- FF. Leaflets sharply and \pm remotely serrate, narrower, digitate. Coastal, northern California to Alaska 5a. *P. gracilis* ssp. *typica*
- EE. Leaves less prominently discolored, pilose, hirsute or tomentulose to glabrate, variously cut, digitate. Alaska to southern California and Colorado 5b. *P. gracilis* ssp. *Nuttallii*
- AA. Anthers subrotund or oval, mostly 0.5 mm. long; leaves digitate or often subpinnate, the leaflets sharply toothed apically, cuneate to base, the pubescence silky, strigose. Subalpine to high alpine; widespread. British Columbia through California to Arizona, east to Colorado and South Dakota 6. *P. diversifolia*

1. POTENTILLA BRUNNESCENS Rydb., Bull. Torr. Club 28:173, 1901

Figure 47

Western Wyoming and northern Colorado, at elevations of 2000 to 2800 m. Type, from Spread Creek, Wyoming, *Tweedy 212*, seen at New York.

The specific name was aptly applied to this plant of yellow-green herbage and tawny pubescence. In Yellowstone Park and at Kamiah, Idaho, a glabrate form of the species is found, but in it the characteristic glands are retained.

We have not cultivated this species in the transplant experiments, so it will not be considered further.

2. POTENTILLA FLABELLIFORMIS Lehm., Stirp. Pug. 2:12, Aug. 1830

Figures 47 and 57, upper

Potentilla gracilis var. *flabelliformis* Nutt. ex Torr. & Gray, Fl. N. Amer. 1:440, 1840.

Potentilla flabelliformis var. *tenuior* Lehm., Rev. Potent. 108, 1856.

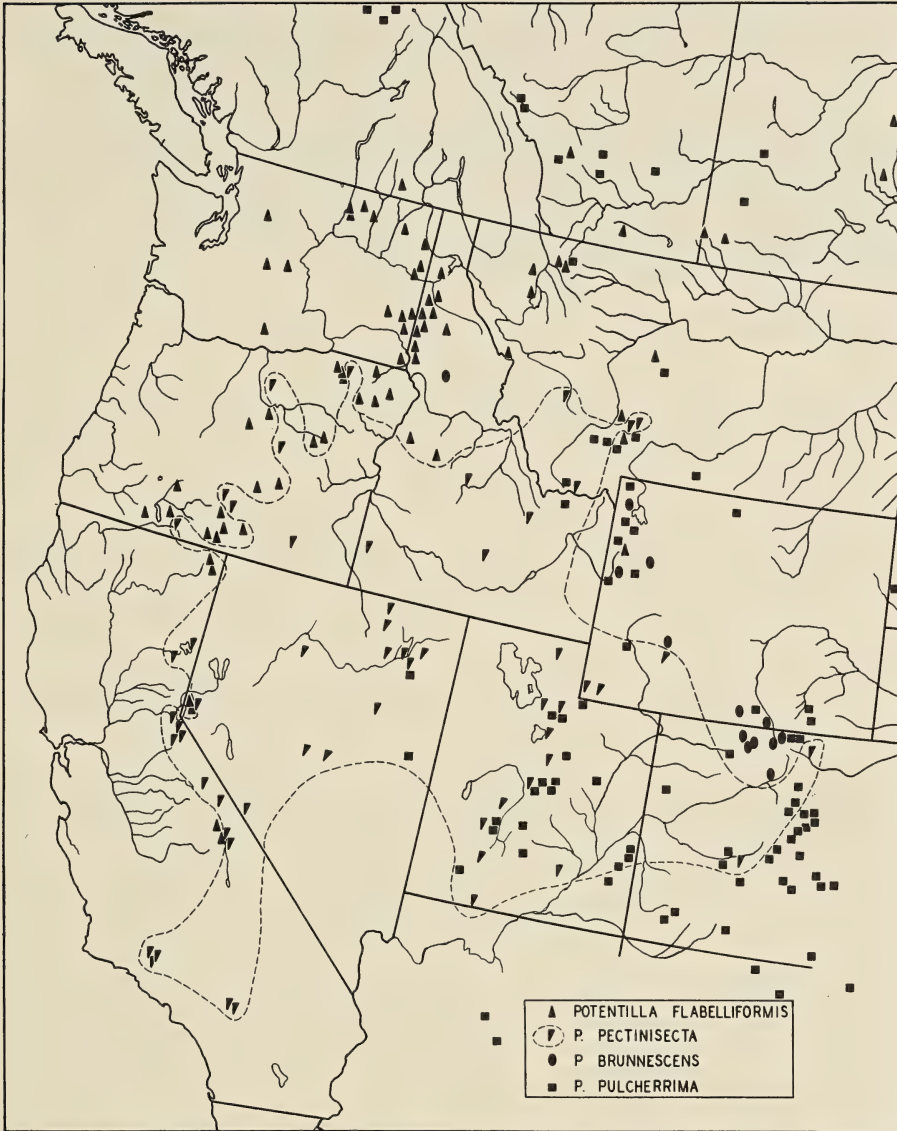


FIG. 47. Distribution of four species of the *Potentilla gracilis* complex as determined from collections in various herbaria.

Potentilla flabelliformis var. *ctenophora* Rydb., Bull. Torr. Club 24:7, 1897.

Potentilla ctenophora Rydb., Mem. Dept. Bot. Columbia Univ. 2:75, 1898.

Potentilla flabelliformis var. *typica* Wolf, Bibl. Bot. 16(71):214, 1908.

Potentilla flabelliformis var. *typica* f. *tenuior* Wolf, *ibid.*

Potentilla longiloba Rydb., N. Amer. Fl. 22:317, 1908. Type, from Lo-Lo, Montana, *Elrod et al.* 110, seen at New York.

Potentilla flabelliformis var. *inyoensis* Jeps., Fl. Calif. 2:189, 1936. Type, from Bishop, California, *Hall & Chandler 7279*, verified at University of California.

Southern Saskatchewan to southernmost British Columbia, southward to northwestern Wyoming, central Idaho, and northeastern California; rare about Lake Tahoe and in Inyo County, California. Lehmann's plate (Monogr. Potent. suppl. 1, pl. 6, 1835) is of a form with strictly digitate leaflets deeply parted into very narrow lobes, like material we have seen from Saskatchewan.

3. *POTENTILLA PECTINISECTA* Rydb., Bull. Torr. Club 24:7, 1897

Figures 47 and 56, lower

Potentilla candida Rydb., *ibid.* 6. Type, from Diamond Valley, Nevada, *Watson 337*, verified at New York.

Potentilla Bakeri Rydb., *ibid.* 31:560, 1904. Type, from Grizzly Creek, Larimer County, Colorado, taken in 1896 by C. F. Baker, seen at New York.

Potentilla Pecten Rydb., N. Amer. Fl. 22:315, 1908. Type, from Bridger Mountains, Montana, *Rydberg & Bessey 4377*, seen at New York.

Potentilla Elmeri Rydb., *ibid.* Type, from Mount Pinos, California, *Elmer 4009*, seen at New York.

Potentilla comosa Rydb., *ibid.* 316. Type, from Bear Valley, San Bernardino Mountains, California, *Parish 3152*, seen at U. S. National Herbarium.

Potentilla gracilis var. *Elmeri* Jeps., Fl. Calif. 2:189, 1936.

Essentially a species of mountainous areas in the Great Basin, southwestern Montana and Wyoming, southern Idaho, eastern Oregon and California, eastward across Nevada and Utah to northwestern Colorado, where it is apparently rare and somewhat atypical. The type, from near Salt Lake City, *Jones 1765*, has been seen at New York.

A form much like this except for the presence of dense tomentum on the leaves, from Alpine County, California, has been named as a species, *P. subvillosa* Rydb. It may prove to be subspecifically distinct from this.

4. *POTENTILLA PULCHERRIMA* Lehm., Stirp. Pug. 2:10, Aug. 1830

Figures 47 and 58

Potentilla pennsylvanica var. *pulcherrima* Torr. & Gray, Fl. N. Amer. 1:438, 1840.

Potentilla Hippiana var. *pulcherrima* S. Wats., Proc. Amer. Acad. 8:555, 1873.

Potentilla filipes Rydb., Bull. Torr. Club 28:174, 1901. Type, from Wahatoya Canyon, Spanish Peaks, Colorado, *Rydberg & Vreeland*, not verified.

Potentilla pulcherrima var. *filipes* Wolf, Bibl. Bot. 16(71):209, 1908.

Potentilla camporum Rydb., N. Amer. Fl. 22:319, 1908. Type, from Black Hills, South Dakota, *Pratt 93*, not verified.

Widespread in mountainous regions, at elevations up to 3500 m., from northern Alberta and British Columbia to southwestern Manitoba, Black Hills, New Mexico, eastern Nevada, and northern Arizona, principally east of Idaho. The type came from the Rocky Mountains between 52° and 56° north latitude (*Drummond*); not seen.

5. *POTENTILLA GRACILIS* Dougl. ex Hook., Bot. Mag. 57:pl. 2984, May 1830.

Figure 48

This species was published probably a few months earlier than Lehmann's species in this group, so if these all belong in one cenospecies, it may properly be called cenospecies *P. gracilis*.

5a. *Potentilla gracilis* Dougl. ssp. *typica* Keck nom. nov.

Potentilla gracilis Dougl. ex Hook., *loc. cit.*

Potentilla longipedunculata Rydb., Mem. Dept. Bot. Columbia Univ. 2:39, 1898.

The type, from Monmouth, Oregon, taken by Susie Howell, in 1893, is an odd form that was apparently injured by a grazing animal and flowered a second time; seen in U. S. National Herbarium.

Potentilla gracilis var. *typica* Wolf, Bibl. Bot. 16(71):211, 1908.

Potentilla gracilis var. *longipedunculata* Wolf, *ibid.*

Potentilla macropetala Rydb., N. Amer. Fl. 22:313, 1908. Type, from Tillamook, Oregon, collected in 1894, by F. E. Lloyd, seen at New York.

Potentilla alaskana Rydb., *ibid.* 318. Type, from Kodiak Island, *Walpole 1201*, seen at U. S. National Herbarium.

A coastal subspecies found from Sanak and Kodiak islands, Alaska, southward to Mendocino County, California. The type was said to have been taken "on the banks of the Columbia and the plains of the Multnomah rivers, where it was discovered by Mr. Douglas." The plate with the original description clearly depicts this form.

This subspecies was not used in the varied-environment experiments, so all the data for the species in the following pages apply to ssp. *Nuttallii*.

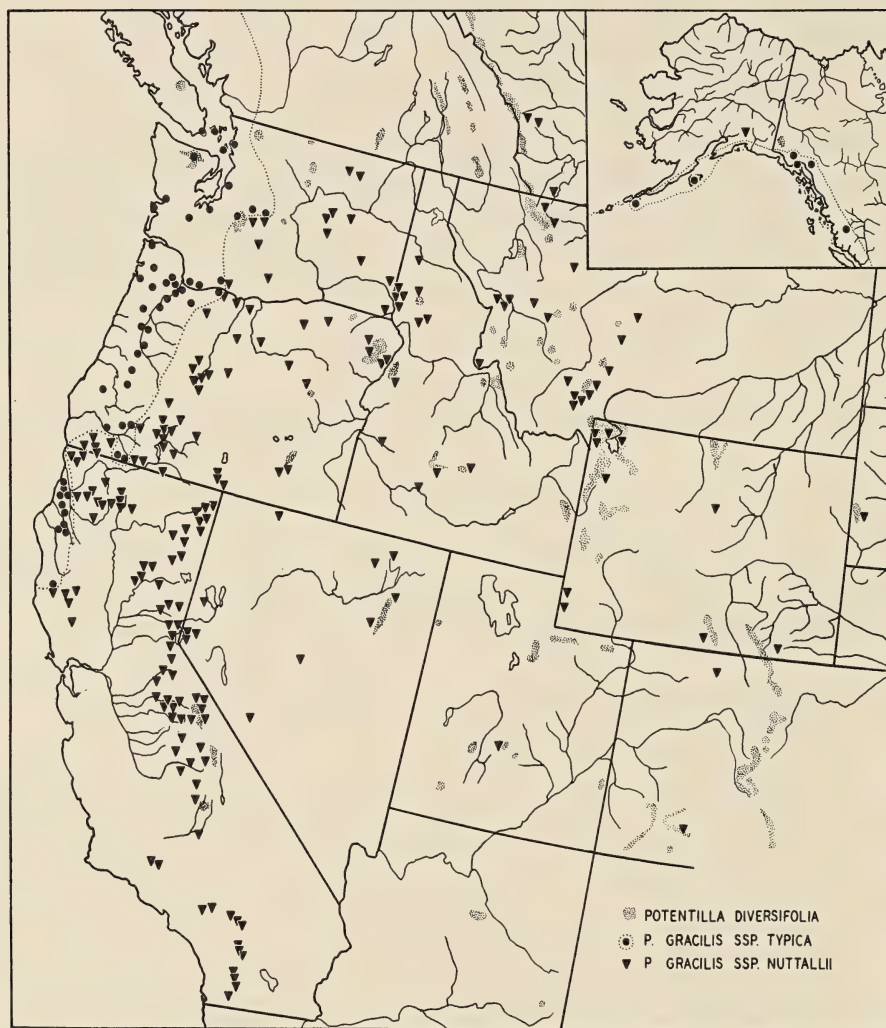


FIG. 48. Distribution of *Potentilla diversifolia* and *P. gracilis* as determined from collections in various herbaria.

5b. *Potentilla gracilis* Dougl. ssp. **Nuttallii** (Lehm.) Keck comb. nov.

Figures 46 (except 1163-1) and 49

Potentilla recta Nutt., Gen. 1:310, 1818; not *P. recta* L., 1753.

Potentilla chrysantha Lehm. in Hook., Fl. Bor. Amer. 1:193, 1832; not *P. chrysantha* Trev., 1818.

Potentilla rigida Nutt., Jour. Acad. Phila. 7:20, 1834; not *P. rigida* Wall., 1828.

Potentilla fastigiata Nutt. ex Torr. & Gray, Fl. N. Amer. 1:440, 1840. This plant,

collected on the "plains of the Rocky Mountains" by Nuttall, seems to belong here, in which case this would be the oldest legitimate name to apply to the group if it were to be treated as a species. Type not verified.

Potentilla Nuttallii Lehm., Stirp. Pug. 9:44, 1851.

Potentilla Blaschkeana Turcz. ex Lehm., Hamb. Gart. & Blumenz. 9:506, 1853.

The type was said to have come from the Russian Settlement (at Fort Ross), California, but the species has not been re-collected there. It is probable that the type was collected on one of the trips back into the Coast Range from Fort Ross, which Russian collectors are known to have made. Here, they would doubtless find ssp. *Nuttallii* rather than ssp. *typica*.

Potentilla Nuttallii var. *glabrata* Lehm., Rev. Potent. 89, 1856.

Potentilla gracilis var. *rigida* S. Wats., Proc. Amer. Acad. 8:557, 1873.

Potentilla gracilis var. *chrysantha* Rydb., Fl. Nebr. 21:16, 1895.

Potentilla etomentosa Rydb., Bull. Torr. Club 24:8, 1897. Type, from California, Fremont 162, not verified.

Potentilla viridescens Rydb., Mem. Dept. Bot. Columbia Univ. 2:69, 1898. Type, from Braggs Creek, Alberta, Macoun 16476, seen at New York.

Potentilla glomerata A. Nels., Bull. Torr. Club 26:480, 1899. Type, from Bear River, Evanston, Wyoming, A. Nelson 4115, verified at Rocky Mountain Herbarium.

Potentilla jucunda A. Nels., Bull. Torr. Club 27:32, 1900. Type, from Green Top, Laramie Hills, A. Nelson 3223a, not seen, but the proposal subsequently placed in synonymy under *P. Nuttallii* by Nelson.

Potentilla Hallii Rydb., Bull. Torr. Club 28:176, 1901. Type, from Pine Ridge, Fresno County, California, Hall & Chandler 182, seen at New York. Plants collected under the same number, at Dudley Herbarium and University of California, differ in several respects from the type, which is a green-leaved form without conspicuous tomentum.

Potentilla permollis Rydb., *ibid.* 175. Type, from Endicott, Whitman County, Washington, collected by A. D. E. Elmer, No. 1830. This is a particularly densely pubescent form that connects with this subspecies through intergrades.

Potentilla gracilis var. *viridescens* Wolf, Bibl. Bot. 16(71):211, 1908.

Potentilla gracilis var. *Hallii* Wolf, *ibid.*

Potentilla Blaschkeana var. *glomerata* Wolf, *ibid.* 212.

Potentilla Blaschkeana var. *permollis* Wolf, *ibid.*

Potentilla diversifolia var. *jucunda* Wolf, *ibid.* 502.

Potentilla angustata Rydb., N. Amer. Fl. 22:311, 1908. Type, from Upper Sacramento River, California, F. H. Foster in 1894, seen at New York.

Potentilla grosseserrata Rydb., *ibid.* 312. Type, from state of Washington, Vasey 322, seen at New York.

Potentilla rectiformis Rydb., *ibid.* Type, from Pullman, Washington, Elmer 69, seen at New York.

Potentilla amadorensis Rydb., *ibid.* Type, from Bear River, Amador County, California, *Hansen 1946*, seen at New York.

Potentilla Parishii Rydb., *ibid.* 313. Type, from Descanso, San Diego County, California, *Parish 4523*, seen at New York. This is a form with deeply cut leaves.

Potentilla glabrata Rydb., *ibid.*

Potentilla dascia Rydb., *ibid.* Type, from The Dalles, Oregon, *Harford & Dunn 1144*, seen at New York.

Potentilla lasia Rydb., *ibid.* 314. Type, from Bear Valley, San Bernardino Mountains, California, *Parish 3252*, not verified.

Potentilla dichroa Rydb., *ibid.* 319. Type, from Old Sentinel (Mountain), near Missoula, Montana, *MacDougal 185*, seen at New York.

Potentilla Hassei Rydb., *ibid.* 329. Type, from Strawberry Valley, San Jacinto Mountains, Riverside County, California (formerly San Diego County), *Hasse 5696*, seen at New York.

Potentilla gracilis var. *Blaschkeana* Jeps., *Man. Fl. Pl. Calif.* 489, 1925.

Montane meadows, from Alaska, where rare, and Alberta southward to the Black Hills of South Dakota, Colorado, and the mountains of southern California; rare east of western Montana and California; common in the coastal states inland from the area occupied by *ssp. typica*.

Both subspecies of *gracilis* are scarcely known from British Columbia, as shown by the map. This may indicate lack of sufficient botanical exploration in that great province, but since this sort of interrupted distribution is not of uncommon occurrence among Pacific Coast species, we suspect that the Pleistocene glaciations were an important factor in accounting for this result, as suggested by Hultén (1937a).

6. *POTENTILLA DIVERSIFOLIA* Lehm., *Stirp. Pug.* 2:9, Aug. 1830

Figures 48 and 55

Potentilla dissecta Nutt., *Jour. Acad. Phila.* 7:21, 1834; not *P. dissecta* Pursh, 1814. Type, collected by Wyeth, on "Kamas Prairie toward the sources of the Columbia," seen at the Academy of Natural Sciences of Philadelphia.

Potentilla glaucophylla Lehm., *Delect. Sem. Hort. Bot. Hamb.* 1836:7, 1836. Type, from the Black Hills, not seen. This represents the common glabrate form of the species, which occurs intermittently with the less frequent, more densely pubescent form. We think that it is without geographical significance and does not represent a distinct ecotype.

Potentilla diversifolia var. *glaucophylla* Lehm., *Stirp. Pug.* 9:44, 1851.

Potentilla dissecta var. *glaucophylla* S. Wats., *Proc. Amer. Acad.* 8:556, 1873.

Potentilla diversifolia var. *genuina* Wolf, *Bibl. Bot.* 16(71):501, 1908.

Potentilla intermittens Rydb., N. Amer. Fl. 22:318, 1908. Type, from Cameron Pass, Colorado, *Baker 25*, seen at New York.

Nearly confined to alpine habitats, but widespread near tree line and above from the Rocky Mountains of Yukon Territory, Alberta, and British Columbia to Colorado, and from Vancouver Island to the Sierra Nevada of central California; known in Arizona only from San Francisco Peaks and the White Mountains, and in New Mexico only from Lake Peak, Santa Fe County; local also in the Black Hills. The type was collected between 52° and 56° north latitude in the Rocky Mountains by Drummond; a possible isotype has been seen at Gray Herbarium.

VARIED-ENVIRONMENT EXPERIMENTS WITH POTENTILLA GRACILIS

Polymorphism is as evident within *Potentilla gracilis* as within *P. glandulosa*. In central California, *gracilis* is not known from the Coast Ranges between Cobb Mountain, Lake County, and Mount Pinos, Ventura County, but is confined to the Sierra Nevada, where it shows diversity in most of its characters.

As previously mentioned, only subspecies *Nuttallii* of *gracilis* has been included in these experiments; it is the only one found in central California. In the Sierra Nevada this form is common on the west slope from 990 m., in the lower border of the yellow pine belt, to slopes above timber line at 3350 m. altitude. It is composed of several ecotypes, but they are not marked by morphological differences as are those of *glandulosa*. *Potentilla gracilis* occurs also on the eastern escarpment of the range, but in the Great Basin, except for widely scattered colonies, it is largely replaced by forms of *P. pectinisecta* and *P. flabelliformis*.

The prominent differences between climatic races of *P. gracilis* ssp. *Nuttallii* in the Sierra Nevada stand out when representatives of these races are grown in a standard environment, as illustrated in figures 46 and 49. Each figure shows plants native at mid-altitude, subalpine, and alpine conditions growing in uniform gardens at Mather. The inverse correlation between plant height and altitude of original habitat is evident in each figure.

While the specimens in figures 46 and 49 illustrate the general trend at different altitudes, they do not depict the complications found in the field, for variation within local populations is often more striking



FIG. 49. Plants of *Potentilla gracilis* from different altitudes, growing in a uniform garden at Mather.

Plant 1155-4 (below), from Mather at 1400 m. ($2n=ca. 103$); 1157-2 (center), from Tuolumne Meadows at 2650 m. ($2n=ca. 70$); and 1159-5 (above), from near Timberline station at 3050 m. ($2n=ca. 64$). Photographs taken in 1937, all shown to the same scale.



FIG. 50. Individual variations in *Potentilla gracilis* from the same populations.

Left: tall and dwarf forms originally from Mather at 1400 m., 1155-7 ($2n=ca. 101$) and 1155-5 ($2n=ca. 63$). Right: tall and dwarf forms from near Timberline station at 3050 m., 1159-6 ($2n=ca. 59$) and 1159-1 ($2n=ca. 84$). Specimens from plants growing in a uniform garden at Mather.

in this species than in *P. glandulosa*. Examples from two localities, Mather and Timberline, are shown in figure 50. The plants from Mather represent extremes from one meadow, in which various gradations also exist. At Timberline the variation is at least as great. Variations in leaf cut, leaflet number, pubescence, and growth habit occur in all combinations. Even appreciable differences in earliness of flowering have been noted among individuals native at Mather and Timberline.

Potentilla gracilis is well adapted for transplant experiments because it is fairly easy to propagate vegetatively and because most



FIG. 51. Modifications in a clone of the mid-Sierran ecotype of *Potentilla gracilis* at three altitudes.

This plant, 1155-4 ($2n = ca. 103$), was dug November 2, 1926, at Mather. The Stanford propagule was transferred from the Berkeley garden in 1929, where it had grown from 1927; the one at Mather was set in 1927, and the one at Timberline in 1930, after being held in a nursery at Berkeley. All specimens were taken in 1935. Note the immaturity of the Timberline propagule, even near the end of the growing season (August 29).

forms survive at all altitudes. Its ecotypes, in general, react much like those of *P. glandulosa*.

MID-ALTITUDE ECOTYPE

Among a number of plants included in the experiments from Mather, at 1400 m. elevation, eight individuals from a meadow were divided and distributed to the three stations. They represented extreme forms of the local variation; six were tall like 1155-7 and two were short like 1155-5, figure 50. Typical modifications of a plant of the tall Mather race are shown in figure 51.

There is an apparent similarity in reaction between the mid-altitude ecotype of *P. gracilis* ssp. *Nuttallii* and the foothill ecotype of *P. glandulosa* ssp. *reflexa*, both native at Mather. Modifications of both are tallest at Mather, somewhat lower at Stanford, and still lower at Timberline. Both flower so late at Timberline that their seed do not ripen. However, the mid-altitude ecotype of *gracilis* survives for several years, while *P. glandulosa reflexa* dies very promptly. It appears, therefore, that the Mather races of the two are not ecologically equivalent. Rather, the Mather race of *gracilis* compares with the rare meadow ecotype of *glandulosa*, ssp. *Hanseni*, also a Mather native that grows intermixed with it in the meadow from which both were taken. Both are taller at Mather than at the other stations (see fig. 28), flower characteristically late, and survive at Timberline.

One of the most striking characteristics of the Timberline modification of the mid-altitude ecotype as compared with the Mather modification is the reduced size of vegetative parts. Height, size of basal leaves, and general dimensions are reduced in approximately the same proportion. Leaf pubescence increases in density at Timberline in about the same degree that leaf area is diminished, and leaves also seem to be somewhat thicker than at Mather. The color of foliage is lighter green than at Mather and the branches are fewer and shorter, resulting in more congested inflorescences, which bear fewer flowers per stem.

Not all mid-altitude plants show so great a degree of dwarfing at Timberline as that shown in figure 51, for in this specimen the dwarfness is somewhat exaggerated by the incomplete development of the inflorescence. This is of equal interest, however, because it shows this plant is still immature toward the end of the growing season at Timberline.

The Berkeley and Stanford modifications of the mid-altitude ecotype are less striking. As seen in figure 51, the Stanford propagule is distinctly shorter than the one at Mather; it has somewhat thicker peduncles and pedicels; its flowers tend to be more congested; and its basal leaves have shorter petioles, somewhat broader leaflets, and more rounded teeth. Also, the leaves are thicker, more heavily veined, and of a deeper color. All these modifications are of minor character and are subject to yearly fluctuations. However, on the basis of composite evidence from ten individuals, accumulated over

periods of from two to seven years, these modifications appear to be typical of the Mather races.

Examples of these modifications are shown in table 17. Here, the length of longest stems, the number of stems, and the date of first flowers are tabulated for representative individuals of the various ecotypes and ecospecies of the *gracilis* complex that are in culture. This offers an opportunity to compare the reactions of various individuals of one ecotype, and of the various ecotypes and ecospecies as a whole. As explained in connection with similar data for *P. glandulosa*, we have chosen to present these data out of the many measurements available, because length of stem is a general indication of the plant's size, number of flowering stems is an expression of its vigor, and the date on which first flowers appear is the most reliable measure of the tempo at which the plant carries on its life processes in different climates—a most important consideration not only for the perpetuation of the race through the production of ripe fruit, but also for the survival of the individual itself.

Individual differences are retained in spite of climatic modifications. Peculiarities in earliness, pattern of veining, number, shape, and arrangement of leaflets, number of teeth on corresponding leaflets, density of pubescence, number and relative length of internodes, and size and color of flower parts, and individual differences in habit and vigor are retained by clone members of each individual at the three stations. The sum total of such characteristics makes possible the recognition of particular individuals, even though modifications brought about by transplanting have been superimposed. Individuals from the same original habitat show differences in degree of modifiability (see 1155-3 and -4 in table 17), and the extent of modification undergoes annual variation, depending upon climatic fluctuations.

Mid-Sierran races of *Potentilla gracilis* brought to Timberline are not always able to flower during the short growing season, and cannot produce ripe fruit. One reason for this is that their stems are killed by the first frost. However, a sufficient reserve of organic food material is apparently synthesized to carry them through the long winters, for they continue to survive year after year. At Berkeley or Stanford, transplants originally from Mather have a longer growing season than at their native habitat. By June, clone members at Stanford have matured ripe fruit, those at Mather are still in flower,

and those at Timberline are still held beneath the ground by retreating snows. In August, Stanford propagules have shed their akenes and begun a slow secondary growth of basal leaves, divisions at Mather are maturing fruit and beginning to shed their seed, and those at Timberline are still developing flower buds. By October, plants at Stanford have slowed their vegetative activity and will soon be dormant, while those at Mather and Timberline are already dormant owing to the onset of cold nights.



FIG. 52. Modifications in a clone of the mid-Sierran ecotype of *Potentilla gracilis* at two altitudes.

The propagule at Mather is becoming dormant after having ripened its crop of fruit, but the one at Timberline has been injured by fall frosts while still in the early flower-bud stage; photographs taken within an interval of three days in early September 1937. This plant, 1155-2, was dug at Mather November 2, 1926, $2n \approx ca. 84-87$, the division at Mather was planted in 1927, and the one at Timberline in 1930, from the nursery at Berkeley.

An illustration of the differences in seasonal reactions is given in figure 52, in which a clone originally from Mather is depicted in the gardens at Mather and Timberline. These propagules were photographed three days apart in early September. Note that the leaves of the clone member at Mather are drying up because the plant has completed its cycle through the long summer at that station and its akenes are shed. The inflorescences nod at Timberline because they have been killed by frosts while still in the bud stage, so that this propagule has no chance to flower there in that year.

TABLE 17

MODIFICATION AND EARLINESS IN CENOSPECIES *POTENTILLA GRACILIS*

NUMBER AND ORIGIN OF PLANTS	YEARS OF DATA	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
		Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
<i>Potentilla gracilis Nuttallii</i> (all Californian):										
Mid-ALTITUDE ECOTYPE:										
1155-3, Mather, 1400 m.....	'35-'36	43.0	90.0	21.5	5.5	30.0	1.5	May 11	Jun. 12	Sep. 1
-4, Same.....	'35-'36	57.5	77.5	23.0	7.0	20.0	3.5	May 7	Jun. 12	Aug. 24
-5, Same.....	'35-'37	41.5	64.0	38.0	9.5	32.5	8.0	May 2	Jun. 1	Aug. 10
-8, Same.....	'35-'37	40.3	78.3	36.0	7.7	24.0	6.7	May 11	Jun. 9	Sep. 12
Means.....		45.6	77.5	29.6	7.4	26.6	4.9	May 7.8	Jun. 8.5	Aug. 27.3
SUBALPINE ECOTYPE:										
1157-1, Tuolumne Meadows, 2650 m...	'35-'36	40.0	67.5	20.5	2.5	35.0	5.0	May 3	May 29	Aug. 22
-2, Same.....	'36-'37	53.5	60.0	36.5	16.5	52.5	5.0	May 2	May 26	Aug. 14
-4, Same.....	'35-'37	48.3	46.0	39.7	3.7	14.0	2.7	Apr. 25	May 30	Aug. 16
-5, Same.....	'35-'37	54.0	65.7	33.7	7.3	30.0	8.7	May 1	May 29	Aug. 15
-6, Same.....	'35-'37	51.0	58.0	34.3	5.0	24.3	10.3	Apr. 25	May 29	Aug. 14
Means.....		49.4	59.4	32.9	7.0	31.2	6.3	Apr. 29.2	May 28.6	Aug. 16.2
ALPINE ECOTYPE:										
1160-2, Mt. Dana, 3150 m.....	'35,'37	27.5	50.0	20.5	4.0	16.0	3.0	Apr. 25	May 23	Aug. 5
1158-3, Tioga Pass, 3030 m.....	'36*	25	26	30	2	7.7	20	May 1	May 25	Aug. 21
1159-1, Slate Creek, 3050 m.....	'36*	40	29	25	4.5	8.7	15.0	May 1	May 26	Aug. 15
-2, Same.....	'36*	40	35	18	6	18.3	3.5	Apr. 28	May 26	Aug. 22
-3, Same.....	'36	55	40	28	2	18	4	May 1	May 21	Aug. 18
-4, Same.....	'35-'36	35.0	46.5	27.0	2.0	13.0	2.0	May 1	May 26	Aug. 18
-5, Same.....	'35-'36	41.5	28.5	29.0	3.5	5.0	15.5	May 1	Jun. 9	Aug. 9
-6, Same.....	'35-'37	38.5	43.0	31.3	4.0	10.7	18.0	May 10	May 29	Aug. 5
-9, Same.....	'36-'37	41.5	37.0	33.5	6.5	6.5	33.5	Apr. 27	May 24	Aug. 14
1161-4, Warren Creek, 2750 m.....	'36-'37	35.5	35.0	23.0	4.5	11.5	12.0	Apr. 27	May 26	Aug. 6
Means.....		37.9	37.0	26.5	3.9	11.5	12.6	Apr. 30.3	May 26.6	Aug. 13.3

* Data on number of stems from additional years.

(Continued on following page)

TABLE 17—Continued

NUMBER AND ORIGIN OF PLANTS	YEARS OF DATA	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
		Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
<i>Potentilla gracilis Nuttallii</i> —Continued										
MISCELLANEOUS:										
1152-1, Pine Ridge, 1520 m.....	'35	45	45	24	4	13	10	May 3	Jun. 7	Aug. 7
1154-1, Mineral King, 2390 m.....	'35-'36	47.5	52.5	25.0	4.5	6.0	2.5	Apr. 17	Jun. 1	Aug. 21
-2, Same.....	'35-'37	42.3	44.0	23.7	3.7	7.0	4.3	Apr. 20	Jun. 4	Aug. 24
1161-1, Leevining, 1980 m.....	'36-'37	43.5	47.5	17.5	20.0	4.5	2.0	Apr. 29	Jun. 3	Aug. 29
1164-3, Westwood, 1065 m.....	'35-'37	42.3	61.0	33.0	33.6	26.7	15.0	May 6	Jun. 15	Aug. 15
<i>Potentilla diversifolia</i> :										
1159-7, Slate Creek, 3050 m.....	'35-'37	29.7	16.3	22.0	6.0	3.7	8.7	Apr. 4	May 24	Jul. 27
-8, Same.....	'36	30	23	1	8	Apr. 10	Jul. 25
1160-6, Mt. Dana, 3440 m.....	'36-'37	14.0	34.5	1	27.5	May 18	Jul. 22
-7, Same.....	'36	20	2	Mar. 8
Means.....		26.6	15.2	26.5	3.0	2.4	14.7	Mar. 28.0	May 21.0	Jul. 24.6
<i>Potentilla pectinisetia</i> :										
1162-3, Benton, Calif., 1730 m.....	'36	65	37	45	5	2	1	May 6	May 27	Sep. 1
<i>Potentilla flabelliformis</i> :										
1163-1, Wells, Nev., 1710 m.....	'35-'37	49.5	77.5	35.0	15.5	32.5	7.5	May 5	Jun. 11	Aug. 29
1165-3, Meacham, Ore., 1120 m.....	'36-'37	32.0	47	32.5	1.5	4.0	May 6	Aug. 27
-4, Same.....	'35-'37	29	51.0	27.3	16.3	1.7	Jun. 1	Aug. 23
-1, Same.....	'35-'37	45.3	82.3	39.0	7.3	41.7	1.7	Apr. 25	May 31	Sep. 2
-2, Same } transitional to <i>P.</i>	'36-'37	50.5	102.5	27.7	7.0	45.0	3.0	May 20	Jun. 21	Sep. 18
-5, Same } <i>gracilis Nuttallii</i>	'35-'37	44.3	74.0	30.7	9.0	27.0	4.3	Apr. 25	May 29	Aug. 21
Means.....		41.8	72.4	32.0	8.1	32.5	3.7	May 4.2	Jun. 6.0	Aug. 30.0
<i>Potentilla pulcherrima</i> :										
1166-3, San Pete Co., Utah, 2440 m.....	'35-'36	46.5	55.0	29.0	4.5	14.0	3.0	Apr. 23	May 26	Jul. 30
1167-1, Pikes Peak, Colo., 2700 m.....	'36	55	65	36	5	40	3	May 7	Jun. 2	Sep. 1
-2, Same.....	'35-'37	51.3	71.3	31.0	8.3	120.0	4.0	May 8	Jun. 8	Aug. 20
Means.....		50.9	63.8	32.0	5.9	58.0	3.3	May 2.7	Jun. 2.7	Aug. 16.7

The unpredictable nature of individual modifications is well illustrated by the two smallest plants dug in the Mather meadow. They remain smaller than the others at Stanford and Mather, but are among the tallest at Timberline. This reversal in relative heights at Timberline is illustrated by 1155-5 in table 17 and is connected with differences in chromosome numbers and earliness. The plant 1155-5 is the only one of this population that is so early at Timberline that it develops to its full capacity. At this station differences in earliness are very much accentuated because of the short season. As is shown in table 17, this plant is nine days earlier than the latest at Stanford, eleven days earlier at Mather, but more than one month earlier at Timberline. The other dwarf from the Mather population (1155-6, not listed in the table) is even smaller than this plant at Mather and tends to be one of the larger plants at Timberline, but it does not parallel it in earliness. On the contrary, it is among the last plants from this population to bloom at Timberline. Both, however, have lower chromosome numbers than the others (compare tabulation on p. 174).

SUBALPINE AND ALPINE ECOTYPES

Plants of *Potentilla gracilis* native at higher elevations in the Sierra Nevada are smaller and earlier at all transplant stations than those from mid-altitudes. Our altitudinal series is not as complete as in *P. glandulosa*, but the samples are sufficient to indicate that there are significant differences between the true alpiners and members of the mid-altitude ecotype, and that plants from subalpine conditions are almost as early as the alpine, but significantly taller. An example of the reactions of a member of the alpine ecotype from near Timberline station is shown in figure 53.

Propagules brought to Mather tend to enlarge all vegetative parts as contrasted with those cultivated at Timberline. Area of leaves and length of stems increase (table 17). Vigor and general dimensions do not differ appreciably in the alpine ecotype, but increase considerably in the subalpine. At Timberline the growth habit is decumbent to ascending, while members of the same clone at Mather are ascending to semi-erect.

At the coastal stations clone members of alpine and subalpine races usually have shorter stems than at Mather. Also, the Stanford modifications have slightly smaller, darker, and duller basal leaves;



FIG. 53. Modifications in a clone of the alpine ecotype of *Potentilla gracilis* at three altitudes.

This plant, 1159-5, was dug September 12, 1929, near Timberline station at 3050 m.; $2n = ca. 64$. The propagules at Mather and Timberline were planted in 1930, and the one at Stanford in 1934 as a division from the propagule at Mather. The specimens were all taken in 1935.

their inflorescences are decidedly fewer and more open; and their stems and peduncles are thicker. Alpine forms grow with fair vigor at Berkeley and Stanford, but not so well as at either mountain station.

Alpine types follow a rapid course of seasonal development similar to that shown by high-altitude types of *P. glandulosa*, and flower an average of one to two weeks earlier than mid-Sierran plants at all the stations. There is a slight although statistically insignificant difference in earliness at all three stations between the plants native at Tuolumne Meadows and those from higher elevations (table 17). Of greater interest is the fact that the native population at Timberline is composed of two races, which, in years with a late season, differ very much in earliness. In the late year 1936 this was especially noticeable (see fig. 62, p. 164), for half of our sample of the alpine population was almost one month later in flowering than the other half. The late plants follow the same annual schedule for flowering as the subalpine plants from Tuolumne Meadows. This difference

in earliness in less noticeable, but still evident, in the average date of first flowers at Timberline as given in table 17. (Plants 1160-2, 1159-5, -6, -9, and 1161-4 belong to the early type.)

Very few plants of *P. gracilis* produce ripe seed at Timberline each year. In fact, only half of the plants originally from the meadow surrounding the Timberline garden itself are able to ripen seed regularly. This is a conspicuous difference between *glandulosa* and *gracilis*—species that ascend equally high in elevation.

The failure of alpine *gracilis* to ripen seed at Timberline every year is due to more than one factor. In the first place, the average flowering date of the alpine ecotype is about ten days later than that of alpine *glandulosa*; this gives the latter a big advantage in an environment with such a short season. In the second place alpine *gracilis* is injured much more severely by early frosts than is alpine *glandulosa*. The stems of some alpine *gracilis* collapse from frost injury, like the ones shown in figure 52, at temperatures that do not affect alpine *glandulosa*. Individual differences are important here, for some early alpine *gracilis* are resistant, while others are not, and some late ones differ similarly. It is clear from this that the capacity to reproduce in such an alpine environment is dependent upon many interwoven factors.

The additional length of growing season at Mather is not utilized by alpine forms of this species so effectively as by corresponding races of *P. glandulosa*, for, after maturing seed, they lapse into a summer dormant period, which is then broken a few weeks later by the development of new basal leaves that continue to develop slowly until the advent of October frosts. A similar period of dormancy takes place at Stanford after flowering in July, and is then followed by new growth in the rosette, which continues until November, at the beginning of winter dormancy. That the excess organic synthates produced by alpine races during the long season at Stanford are probably respired almost as fast as they are built up is suggested by the tendency for their clone members to be less vigorous and smaller than those at Mather and Timberline.

COMPARISON OF THE SIERRAN ECOTYPES

Three ecotypes of *Potentilla gracilis Nuttallii* are found in the central Sierra Nevada, as shown in the preceding pages. These differ by a series of characters that may be quite complex. Two characters

that may be most important are size and earliness. A statistical measure of the differences in these characters is given by the mean length of longest stems and mean dates of earliest flowers, as determined by measurements from Mather and Timberline.

LENGTH OF LONGEST STEMS (CM.)

	Mather	Timberline
Mid-altitude ecotype, from 1440 m. elevation, 7 plants (15 observations).....	74.86 \pm 6.70	31.30
Subalpine ecotype, from 2750 m. elevation, 6 plants (18 observations).....	58.55 \pm 3.24	30.68
Alpine ecotype, from 2750-3150 m. elevation, 11 plants (23 observations).....	38.40 \pm 2.07	26.17
Differences in cm. at Mather:		
Mid-altitude minus subalpine.....	16.31 \pm 7.44 (t = 2.192, barely significant)	
Mid-altitude minus alpine.....	36.46 \pm 7.01 (t = 5.201, highly significant)	
Subalpine minus alpine.....	20.15 \pm 3.84 (t = 5.247, highly significant)	

DATE OF FIRST FLOWERS

	Mather	Timberline
Mid-altitude ecotype, as above.....	June 11.1 \pm 1.96	Aug. 28.3 \pm 3.47
Subalpine ecotype, as above.....	May 28.5 \pm 0.58	Aug. 16.8 \pm 1.55
Alpine ecotype, as above.....	May 26.6 \pm 1.48	Aug. 13.5 \pm 1.91
Differences in days at Mather:		
Mid-altitude minus subalpine.....	14.64 \pm 2.04 (t = 7.176, highly significant)	
Mid-altitude minus alpine.....	16.54 \pm 2.46 (t = 6.724, highly significant)	
Subalpine minus alpine.....	1.9 \pm 1.59 (t = 1.195, insignificant)	
Differences in days at Timberline:		
Mid-altitude minus subalpine.....	11.5 \pm 3.80 (t = 3.026, highly significant)	
Mid-altitude minus alpine.....	14.8 \pm 3.96 (t = 3.737, highly significant)	
Subalpine minus alpine.....	3.3 \pm 2.96 (t = 1.115, insignificant)	

Individual plants within each of the three ecotypes differ considerably in regard to length of stem as shown by the high standard errors. By the same criterion, earliness is much less variable within the ecotype, especially at Mather.

This statistical comparison emphasizes that morphological differences, such as length of stem, are not rigidly linked with physiological differences, as exemplified by earliness. The subalpine ecotype is intermediate in stem length between the mid-altitude and the alpine, but is almost as early as the alpine ecotype, whose members are much smaller. Likewise, the tall forms of the mid-altitude ecotype from

Mather are late, but the low forms from the same locality diverge: one is late like the tall forms, the other is early.

The capacity for modification varies from one plant to another even within a population or an ecotype, as is shown in figure 54. Here

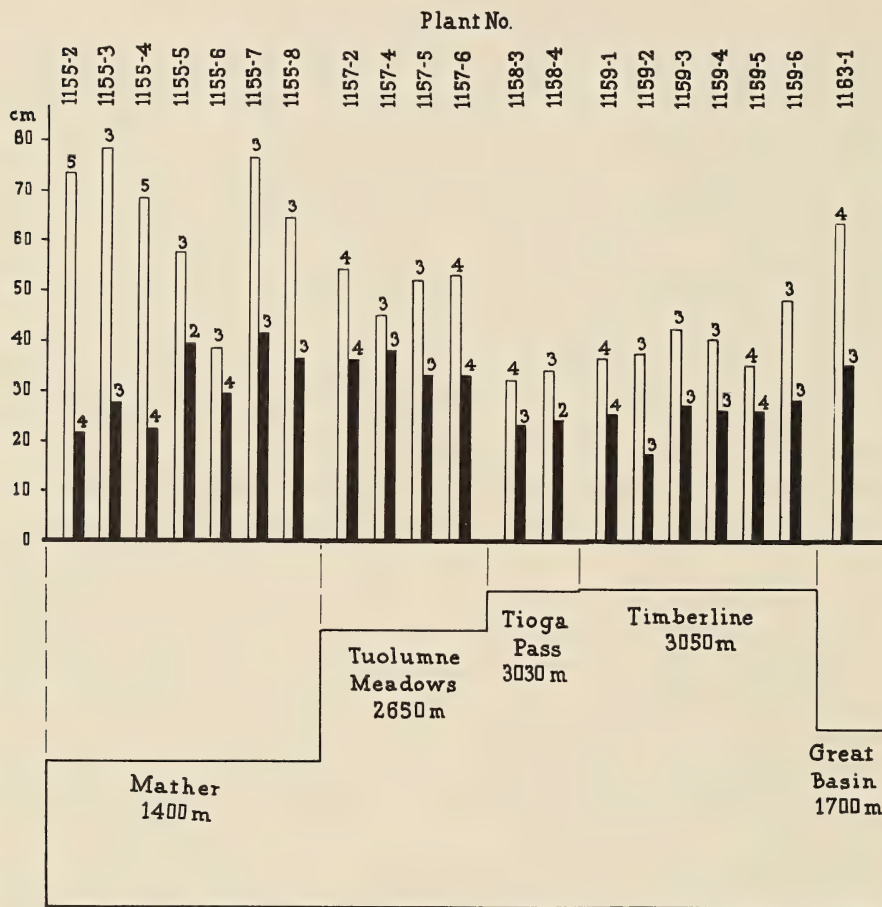


FIG. 54. Heights of clone members of the *Potentilla gracilis* complex at Mather (white columns) as compared with those at Timberline (black columns).

Each pair of columns represents one individual. The numerals above each column indicate the number of years averaged in determining the heights. The original localities and their elevations are also indicated. All the plants represented are *P. gracilis* ssp. *Nuttallii* except the Great Basin plant, 1163-1, which is transitional to *P. flabelliformis*.

mean lengths of stems at Mather and Timberline are plotted for a series of plants of the mid-altitude, subalpine, and alpine ecotypes. One plant of a Great Basin ecospecies, *P. flabelliformis* (1163-1), is

also included. It is evident that the tall plants, which are mostly of the mid-altitude group, are the most modifiable. This graph shows also that differences in capacity for growth are brought out far better in the Mather than in the Timberline environment.

DISCUSSION. In *Potentilla glandulosa* earliness is genetically linked with morphologic characters, and several ecotypes can be recognized by their morphology. There is no indication of such correlation in *P. gracilis Nuttallii*. Pubescence is one of the best indicators of genetical recombination in *gracilis*, for an almost endless number of recombinations as to type, density, and distribution of pubescence is found in the individual population, yet none of these is correlated with earliness. The mode of occurrence of these recombinations indicates that they have no taxonomic value, nor can they be of major ecologic importance to the plant. Their presence, however, is strong evidence that sexual reproduction is possible.

Ecotype differentiation, therefore, appears to progress in this group by hybridization and selection irrespective of apparent partial asexual propagation. Selection has sifted out certain combinations of characters, such as relative earliness, frost resistance, and plant size. Other factors being alike, the early and frost-resistant plant is probably the best fitted for high elevations, but a plant that is either early or frost-resistant is better able to survive there than one that is neither. The fitness of a plant is determined not by a single advantageous factor, but by the interaction of all its factors.

Members of ecotypes characteristic of certain elevations pioneer at other elevations, as they also appear to do in *P. glandulosa*. Thus the late-flowering plants of the Slate Creek Valley population (1159-1, -2, -3, -4, for example, in table 17) are possibly either pioneers from subalpine populations, or evolutionary forerunners of those alpine plants that are early even in years with a late season. Similarly, plants are found at mid-altitudes that react like those from much higher elevations. Plant 1155-5 (see fig. 50), in the Mather population, is of low stature, is early, and reacts like the subalpine ecotype, of which it may even be a representative. This view is supported by the fact that plants of this ecotype thrive very well when transplanted to Mather. If this individual represents a migrant from higher elevations, the equally small but tardy plant, 1155-6, might have arisen by hybridization with the taller late form.

If evolution is constantly going on, situations of these sorts are to be expected. Analyses of natural populations should disclose plant groups in all stages of differentiation. Then, with all the evidence properly pieced together, we should have before us a picture of an evolving, living world.

OTHER SPECIES OF CENOSPECIES *POTENTILLA GRACILIS*

The related species do not all follow the same pattern as *Potentilla gracilis* in their reaction to transplanting. They are all modifiable, but to different degrees. Fewer individuals of these species have been investigated, so a detailed description of their clones at the three stations is not warranted, but some salient features of their reactions will be considered.

POTENTILLA DIVERSIFOLIA LEHM. This exclusively alpine species reacts in opposite fashion to the alpine ecotypes of both *P. gracilis Nuttallii* and *P. glandulosa nevadensis*. In these, the individuals increased in height when moved down the mountains to Mather, but *P. diversifolia* decreases markedly, as shown in figure 55 and table 17 (p. 144). It increases in height again at Stanford, but this is not correlated with an increase in vigor, as indicated by the low number of stems produced. It flowers very poorly at Stanford, as discussed below.

There is some individual morphological variation in this species, as is seen from figure 55, but on the whole there is far less than in *Potentilla gracilis*. *Potentilla diversifolia* may be found in natural populations with *P. gracilis*, to which it shows considerable superficial resemblance, but among other differences it flowers much earlier. Table 17 shows that it is one month earlier than alpine *gracilis* at Stanford, six days earlier at Mather, and three weeks earlier at Timberline. Furthermore, years with a late season do not delay it at Timberline (see fig. 62). The contrast between these species is noticeable in the natural populations on the rocky slopes around Timberline station. The alpine *gracilis* is in bud or first flowers when *diversifolia* has shed almost all its petals.

This difference in earliness is the more impressive because *diversifolia* produces just as long and as many stems at Timberline as the alpine *gracilis*. It starts its spring activity no earlier than the other, but expands its embryonic flowering stems simultaneously with the

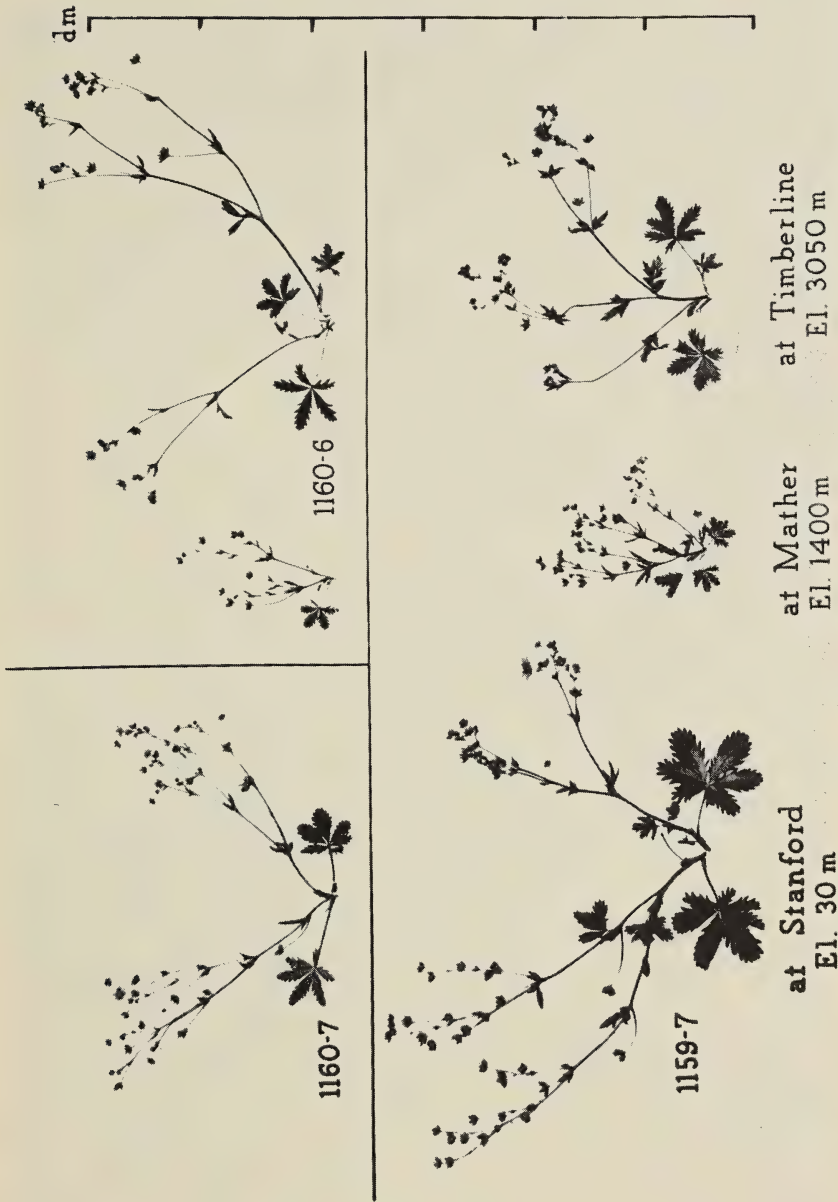


FIG. 55. Modifications in clones of the alpine *Potentilla diversifolia* at three altitudes.
Below: plant 1159-7, dug August 1, 1933, near Timberline station, at 3050 m.; $2n = ca. 101$. Clone members were set at the three stations in 1934. *Above:* plants 1160-6 ($2n = ca. 90-91$) and -7, both dug August 20, 1933, on Mount Dana, Yosemite Park, at 3440 m.; -7 was planted at Stanford, and clone members of -6 at Mather and Timberline, in 1934. The specimens were all taken in 1936.

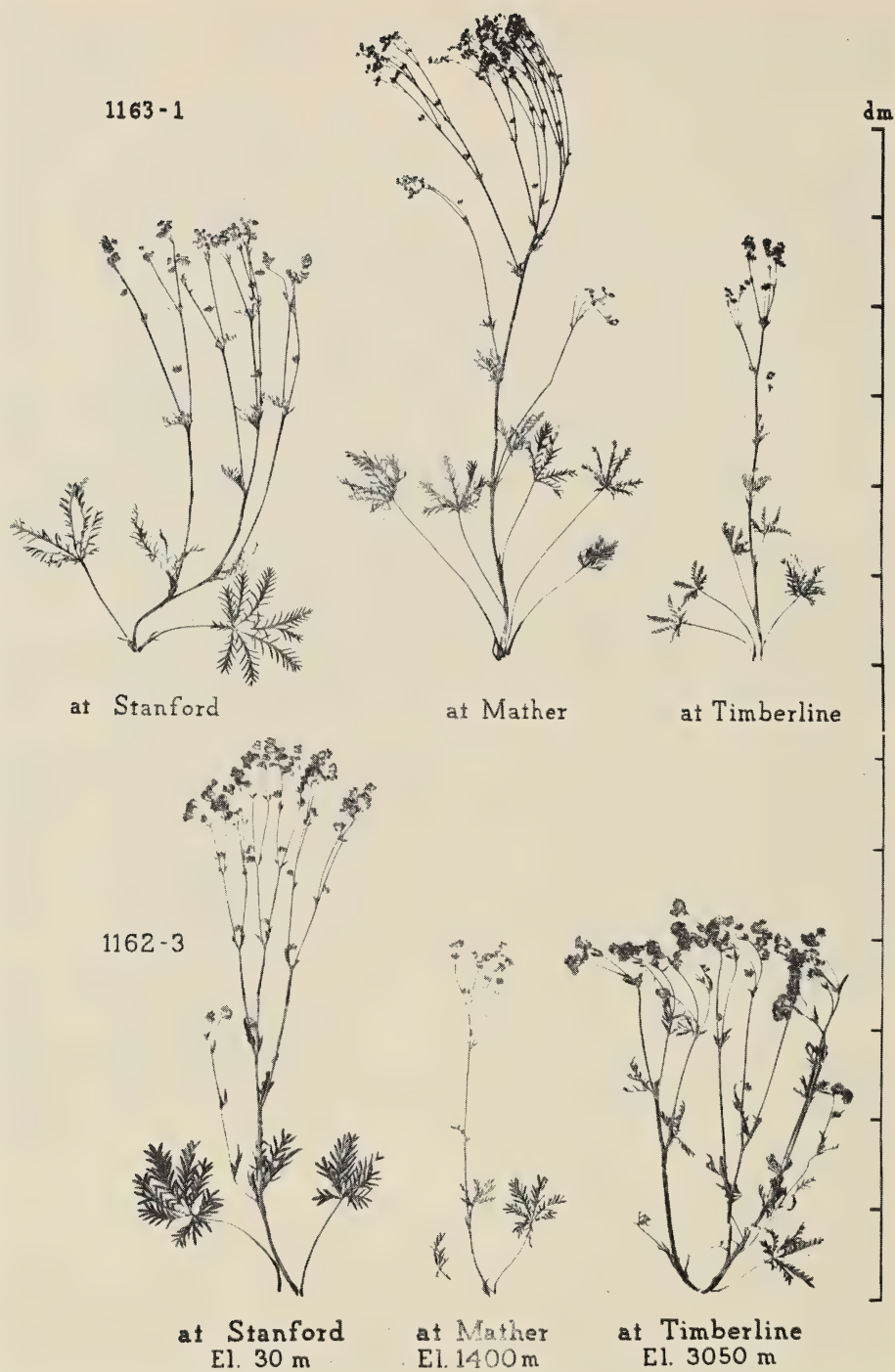


FIG. 56
(Legend on opposite page)

leaves, whereas alpine *gracilis* generally produces a small rosette of fully expanded leaves first. The earliest plants of the latter, however, have a similar tendency to precocity.

The chromosome numbers of *diversifolia* are higher than in the alpine and subalpine ecotypes of *gracilis*, namely, $2n=ca. 83$ to 101 in different plants of *diversifolia* as against $ca. 54$ to 84 in four alpine and subalpine plants of *gracilis*, two of which were of the early alpine form. Obviously, a high chromosome number is not in this case associated with lateness, as it is within *gracilis*.

Considering its reactions, *P. diversifolia* is a truly alpine species well suited to the short season of its native environment. It emerges from the ground as soon as the snows melt, and, at a rapid rate, produces flowering stems apparently from food materials stored in the fleshy taproot during the preceding summer. It matures its seed every year regardless of the abnormalities of the season. Since it is even more frost-resistant than alpine *gracilis*, it is not surprising to find it at higher elevations—as high as 3500 m.

POTENTILLA PECTINISECTA RYDB. This interesting Great Basin species reacts similarly to *P. diversifolia* in the varied-altitude gardens, for it produces least bulk at Mather. However, it is difficult to keep in culture at any of the three stations, so the data relate to three plants only, all native at Benton, Mono County, California, at 1730 m. elevation.

At Stanford this species becomes much more robust than in its native habitat and produces longer stems than any other member of *cenospecies gracilis*, but it does not flower regularly or survive very well. It is shown in figure 56, plant 1162-3. The Mather modification is short and slender, similar in appearance to the species in its native desert flats. The Timberline modification, again, is robust

FIG. 56. Modifications in clones of *Potentilla pectinisecta* (below) and *P. flabelliformis* (above) at the three transplant stations.

Below: plant 1162-3, dug July 22, 1929, at Benton, Mono County, California, at 1730 m.; chromosomes paired, $n=21$. The propagules were set at Stanford in 1934, at Mather in 1930, and at Timberline in 1935. Specimens were taken in 1936 except that the one from Mather was taken in 1932.

Above: plant 1163-1, dug August 20, 1925, at Wells, Elko County, Nevada, at 1710 m.; $2n=ca. 60-65$. This plant is *P. flabelliformis* transitional to *P. pectinisecta*. The Stanford propagule was moved from Berkeley in 1929, where it had grown since 1926; the others were set at Mather in 1927, and at Timberline in 1930. Specimens were taken from Stanford and Timberline in 1935 and from Mather in 1936.

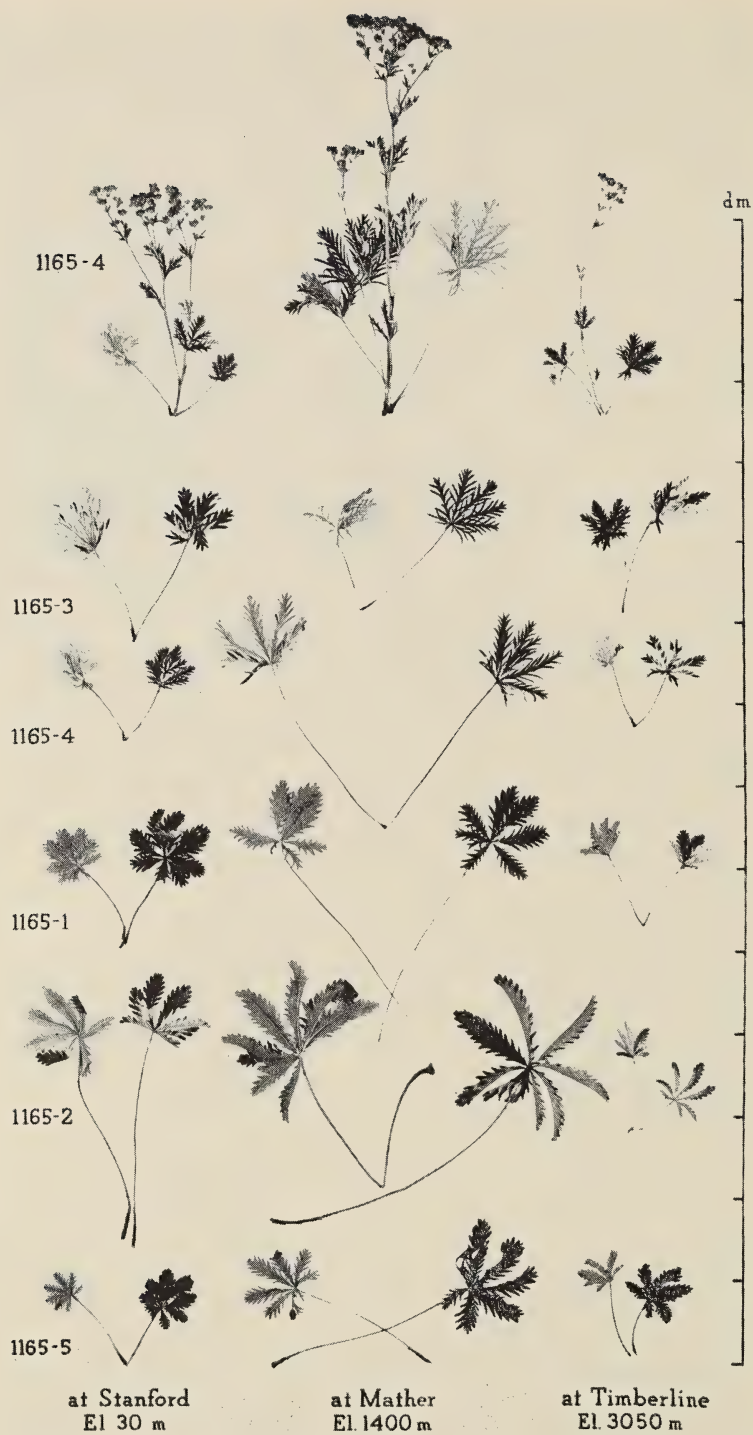


FIG. 57
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and very vigorous; also, it is taller than any other species of this complex, as is shown in the graph, figure 59. *Potentilla pectinisecta* survives moderately well at Mather and Timberline, but is unable to produce ripe seed at the latter station even in years with an early season. In earliness at all three stations it compares closely with the mid-altitude ecotype of *gracilis Nuttallii*.

Cytologically, two plants of the Benton population were regular with 21 pairs of chromosomes in meiosis, a unique situation in this cenospecies otherwise characterized by chromosomal irregularity. Although tests have not been made, the expectation would be that this species reproduces sexually. It is rather surprising to find the cytologically more primitive and probably sexual ecospecies of the *gracilis* complex in the climatically specialized Great Basin desert region.

POTENTILLA FLABELLIFORMIS LEHM. This species, of the northern Great Basin, lives in an environment similar to but less extreme than that of *P. pectinisecta*. Morphologically, also, these species resemble each other. But instead of reacting like *pectinisecta* and *diversifolia*, *flabelliformis* follows the pattern of the mid-altitude ecotype of *P. gracilis Nuttallii*. This can be seen in figure 56, plant 1163-1, and in table 17, page 144. It is tallest at Mather. At Timberline it produces ripe seed only in the exceptionally early years, like 1931 and 1934, but it survives very well and is more frost-resistant than the mid-altitude ecotype of *gracilis*. A typical plant of this species is 1165-4, shown in figure 57.

Like practically all the members of the cenospecies, *P. flabelliformis* appears to hybridize with *gracilis Nuttallii* where they meet. Such a hybridizing population from Meacham, Oregon, is represented in table 17 and figure 57. Hybrids and partial recombinations were in evidence with the more abundant parental types. One clone in flower, and pairs of basal leaves of five clones in this figure illus-

FIG. 57. Modifications in clones of *Potentilla flabelliformis* at three altitudes as illustrated by basal leaves.

The five individuals, 1165-1 to -5, were dug September 1, 1927, at Meacham, Blue Mountains, Oregon, at 1120 m. The flowering specimens in the top row (1165-4) and the upper rows of leaves (1165-3 and -4) represent typical *P. flabelliformis*; $2n = ca. 62-64$ in both. The lowest three (1165-1, -2, and -5) are possibly hybrid recombinations, transitional to *P. gracilis Nuttallii*; the chromosome numbers of -2 and -5 are $2n = ca. 62-65$. The specimens were taken in various years, mostly 1935 to 1937.

trate something of the variations found, and the extent of the modifications. No plants of *gracilis Nuttallii* from this locality were included in the transplant experiments. A classification of a small sample of twenty-seven plants at this locality has given the following result:

<i>flabelliformis</i>	10	(leaflets strongly discolored, pinnatisect, the lobes narrow; like 1165-3 and -4)
<i>gracilis Nuttallii</i>	8	(leaves green both sides, merely lobed, the lobes wider)
Large intermediates	5	(very robust; leaflets lobed to cleft, \pm discolored although slightly tomentose on both sides; like 1165-1 and -2)
Small intermediates	4	(small plants; leaflets discolored, but not pinnatisect; similiar to <i>gracilis typica</i> but a recombination; 1165-5 represents this type)

Each of the four groups showed considerable variation. The parental species were much more preponderant in the population than the tabulation shows, for a special effort was made to tabulate all plants suspected of being hybrids.

The presence of these intermediates at Meacham indicates that *P. gracilis* and *P. flabelliformis* are closely enough related to hybridize and exchange genes. Such evidence of hybridization is commonly found where two closely related ecospecies meet. The presence of intermediates and recombinations also suggests that sexual reproduction is possible, even though about 10 to 20 chromosomes are left unpaired during meiosis in all the plants investigated of this population. These plants were approximately nonaploid ($2n=ca. 63$), irrespective of whether they were pure *flabelliformis* in appearance or of hybrid origin, as, for example, the gigantic 1165-2. The extreme lateness of this plant is very noticeable; at all three stations it is approximately one month later than the other plants of this population (table 17). This difference is consistent year after year, as figures 61 and 62 show.

POTENTILLA PULCHERRIMA LEHM. This Rocky Mountain species is as variable, both cytologically and morphologically, as the other species of this complex. Only three plants have been studied intensively in our gardens, two from Pikes Peak, Colorado (1167), and one from the Wasatch Mountains, Utah (1166-3), all from high, although not alpine, elevations. The plants from Pikes Peak are more robust and later flowering than the Wasatch plant, namely, one to two weeks

later at Stanford and Mather and about one month later at Timberline (table 17, p. 144). This difference at the alpine station was most pronounced in the critical year 1936, when the Pikes Peak plants were delayed like most strains of *P. gracilis* (fig. 62), whereas the Wasatch plant was as early as *P. diversifolia* and the early half of the alpine population of *gracilis*. Accordingly, even in this very late year the Wasatch plant ripened its seed at Timberline, but the Pikes Peak plants are able to do so only in years with an early season (fig. 67). Both strains, however, follow the same pattern of reactions at the three stations in regard to other characters, such as length of stems. Like *P. gracilis*, they grow tallest at Mather, although the difference between the Stanford and Mather modifications is slight. Figure 58 shows the modifications of one of the Pikes Peak plants at the three stations. All three plants of this species become considerably dwarfed at Timberline, yet they survive well there. Table 17 shows that they produce by far the greatest number of flowering stems at Mather, where they are very vigorous. All are more frost-resistant than mid-altitude and some subalpine forms of *P. gracilis*.

The great difference in earliness between the two strains of *pulcherrima* when grown at Timberline indicates significant dissimilarities in their physiological composition. There are also cytological differences. The Wasatch plant is decaploid ($2n=ca. 70$), with fair pairing of the chromosomes, and has an abundance of good pollen with very few dwarf grains. It is probably sexual. The plants from Pikes Peak, on the other hand, are very irregular in meiosis, but differ in their number of chromosomes, with $2n=ca. 108$ in 1167-1 and $2n=ca. 70$ in 1167-2.

COMPARISON OF THE ECOSPECIES AND THE ECOTYPES

For the biologist who studies the ecologic differentiation of a ceno-species like the *Potentilla gracilis* complex, ecotypes and monotypic ecospecies have the same value. The ecotype is his ecologic unit. He is interested in the factors that govern the fitness of the ecotype for its particular environment rather than the morphological characters that happen to be correlated with the ecological units. The internal barriers that prevent ecospecies from freely interchanging their genes have evolutionary and taxonomic importance, but are inconsequential in determining the fitness of a form to its environment.



FIG. 58. Modifications in a clone of *Potentilla pulcherrima* at three altitudes. This plant, 1167-2, was dug in September 1922, at Pikes Peak, Colorado, at 2700 m.; $2n = ca. 71$. It was brought to Mather, where it has been grown ever since. Propagules taken from it were planted at Timberline in 1933, and at Stanford in 1934. The specimens were all taken in 1936.

In the present complex, several ecotypes of *P. gracilis* can be recognized only by experiment, and are not marked by distinctive structural differences which would permit them to be treated as subspecies. Nevertheless, the analyses show that these units are just as important as the ecotypes of *P. glandulosa* that have received sub-specific names as a consequence of their morphological distinctions. Their distinction is based on both physiological and quantitative structural differences. In attempting to discover the composition of the complex network of plants included in such a cenospecies as the

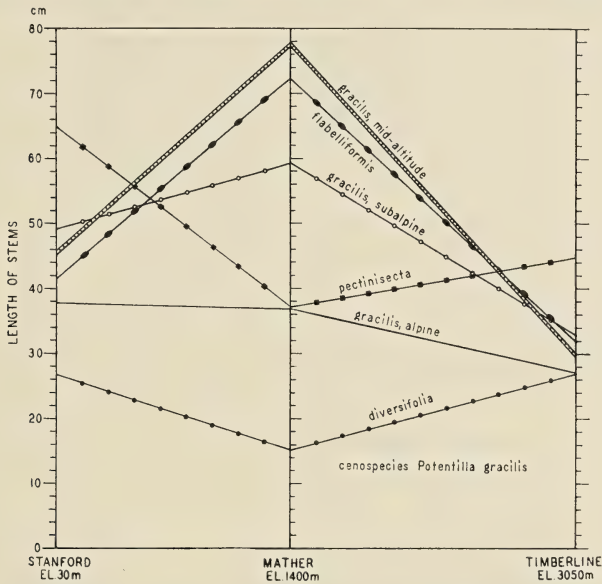


FIG. 59. Modifications in length of stems in clones representing ecotypes and ecospecies of the *Potentilla gracilis* complex at the transplant stations.

The data are averaged from the years 1935 to 1937 for the plants listed in table 17.

present one, it is the reality of their differentiation that matters, and it is relatively unimportant whether or not the units are morphologically recognizable.

DIFFERENCES IN LENGTH OF STEMS AND EARLINESS. These differences at the three transplant stations are summarized for several ecotypes and ecospecies in figures 59 and 60. Figure 59 brings out the distinctions in stem length between the three Sierran ecotypes of *Potentilla gracilis*, which become particularly prominent at Mather. It also depicts the complete reversal in behavior between the morphologically similar Great Basin ecospecies, *P. pectinisecta* and *P.*

flabelliformis (fig. 56). The dwarf stature of the alpine *P. diversifolia* at the three stations, which is especially marked at Mather, is also obvious.

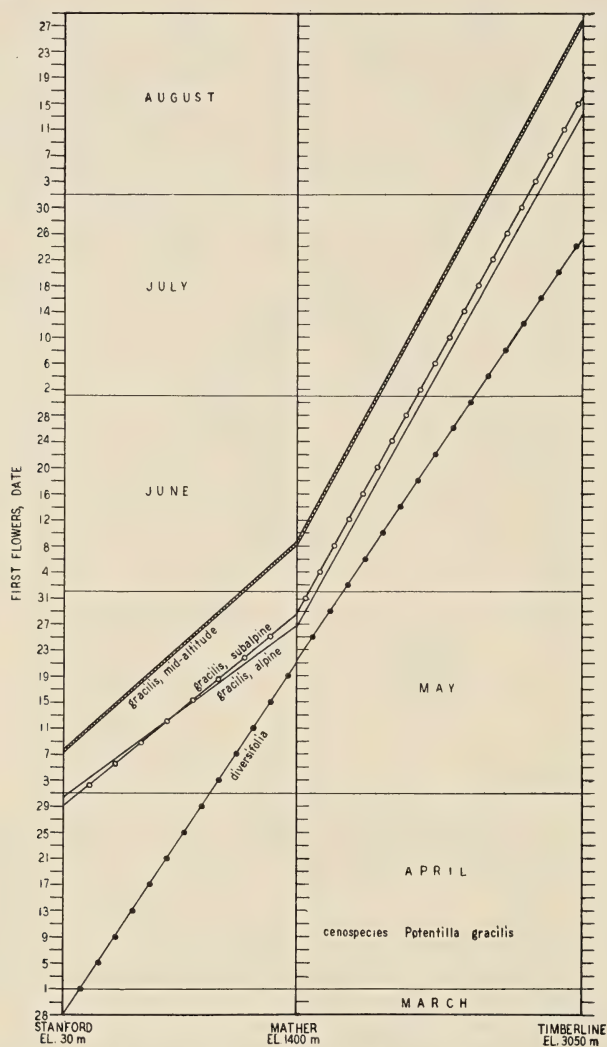


FIG. 60. Modifications in date of first flowers in clones representing ecotypes and ecospecies of the *Potentilla gracilis* complex at the transplant stations. Data from the same sources as in figure 59.

Although there is a significant difference in stem length between the three Sierran ecotypes of *gracilis*, the graph of earliness (fig. 60) shows that only the mid-altitude ecotype is distinctive in regard to flowering time. The subalpine and alpine ecotypes flower at about

the same time at all three stations. *Potentilla diversifolia* is in a class by itself in regard to earliness even as it was for stem length.

Differences in stem length are accentuated at Mather, but differences in earliness are more pronounced at Stanford and Timberline, not at Mather. This again demonstrates that while many racial differences may be discovered by studying plants in one uniform garden, others will be disclosed only as the plants are subjected to other environments, such as the varied climatic gardens of the present experiments.

Individual years differ in the timing of their seasons, and the plants of cenospecies *P. gracilis* respond to these annual fluctuations in a manner similar to that of plants of *P. glandulosa*. The earliness of the ecotypes and ecospecies of the *gracilis* complex is compared graphically in figures 61 and 62. In the first of these, comparisons are made at Mather for the years 1934 to 1937; in the second, similar comparisons are made at Timberline for these years and for 1932 in addition. Like the forms of *P. glandulosa*, most of these groups respond to the early seasons of 1934 and 1936 at Mather (1934 was obviously the earlier of the two). At Timberline, too, the average reaction indicates that 1934 was a very early year, but 1936 was peculiarly late. A few forms, however, namely, *P. diversifolia*, part of the alpine population of *gracilis*, and the Wasatch Mountains plant of *pulcherrima* (1166-3), not only were undelayed in 1936 at Timberline, but were a little earlier than in 1935, which, on the whole, was a more average year. The implications of these differences in reaction patterns have been discussed under the respective species in the preceding pages.

The various groups of plants for the most part follow the fluctuations of the years uniformly and tend to retain their relative positions in the flowering time scale. The small and early 1155-5 from Mather is consistently earlier than the tall plants of the same population (fig. 61). Also, the late *flabelliformis* hybrid (1165-2) is always much later than the other plants of that species, and the representatives of two populations of *pulcherrima* are always clearly distinct in this character at both stations (figs. 61, 62).

Differentiation in regard to earliness, then, is found between ecospecies (*P. diversifolia* versus *P. gracilis*), between ecotypes of one ecospecies (as in *P. gracilis*), and between plants of one population. In the last case the evidence indicates that selection is still incom-

plete. Individuals of a population that deviate spectacularly from the average are usually few, but their presence there is of interest, for it indicates that they can compete in a population with plants of a different constitution. It emphasizes that the differentiation of an

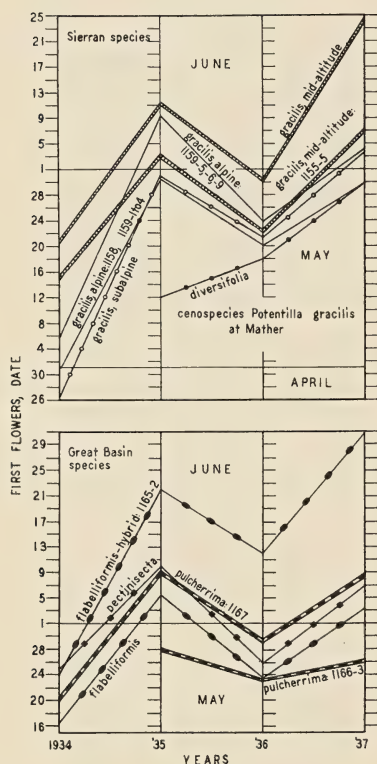


FIG. 61

Yearly variations at Mather (fig. 61) and Timberline (fig. 62) in earliness in clones of various groups of the *Potentilla gracilis* complex.

The graphs are plotted from observations made on the same clone members in successive years for the plants listed in table 17.

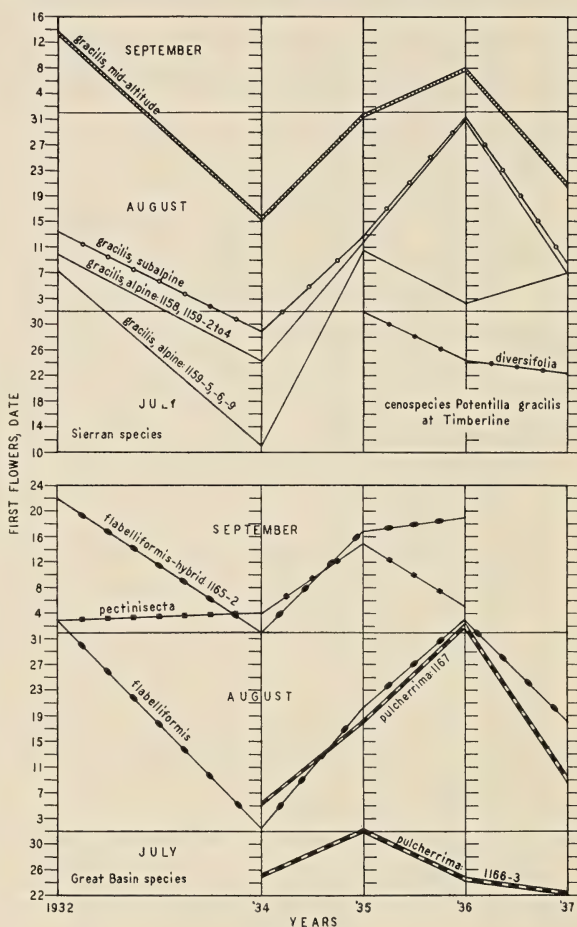


FIG. 62

ecotype is a gradual process, and that its stage of development is expressed in the proportion of the major biotypes of which it is composed.

Finally, there is as much or even more differentiation in earliness between ecotypes of one species than there is between different spe-

cies. This is a simple reflection of the fact that the ecotype is the natural ecologic unit. The basis for species is their genetic separation, but the basis for ecotypes is their environmental fitness.

EFFECT OF DIFFERENCES IN LIGHT AND MOISTURE. *Potentilla gracilis* and its allies respond to differences in light and moisture in the same way that *P. glandulosa* does. Shade tends to increase stem length and leaf size and to decrease the number of stems. This is seen in figure 63, in which propagules of a clone of the subalpine ecotype of *P. gracilis* (1157-2) and one of *P. flabelliformis* (1163-1) are shown as they appear in the dry sun and dry shade plots at Mather. Vigor and bulk are also decreased in shade, although the size of corresponding parts is increased. Shade also decreases leaf thickness, density of pubescence, thickness of petioles and veins, stems, and pedicels, and the mechanical strength of stems, resulting in a more decumbent habit. As in *glandulosa*, shade tends to inhibit flower production.

The more densely pubescent individuals in particular are strikingly less hairy in shaded gardens. In many plants reduction in density of pubescence appears to correspond to the increase in leaf area, but some of the silvery-tomentose forms of *P. pectinisecta* and *P. flabelliformis* have less pubescence in shade than can be accounted for on the basis of wider spacing on a larger leaf.

Transplants of this cenospecies are more vigorous in the moist than in the dry gardens at Mather. A larger number of basal leaves and stems are produced. In the moist sun garden, where practically all forms of this cenospecies attain their best growth, plants originally from Mather become luxuriant. In this plot, basal leaves of some plants have interstitial growth of the petiole between the lowermost leaflets, so that the leaves become subpalmate instead of strictly palmate. This is a character that has been used by monographers of the genus to distinguish major divisions. It should be noted that in nature the leaves of *P. gracilis* are consistently palmate, while those of *pulcherrima* and *diversifolia* vary in this respect.

Clone members in dry and moist gardens are often so similar in appearance that herbarium specimens taken from them can scarcely be distinguished, but those from sun and shade gardens almost always show recognizable differences.

Data in the water-light series were obtained from seven plants of *P. gracilis*, namely, two each of the mid-altitude and subalpine and

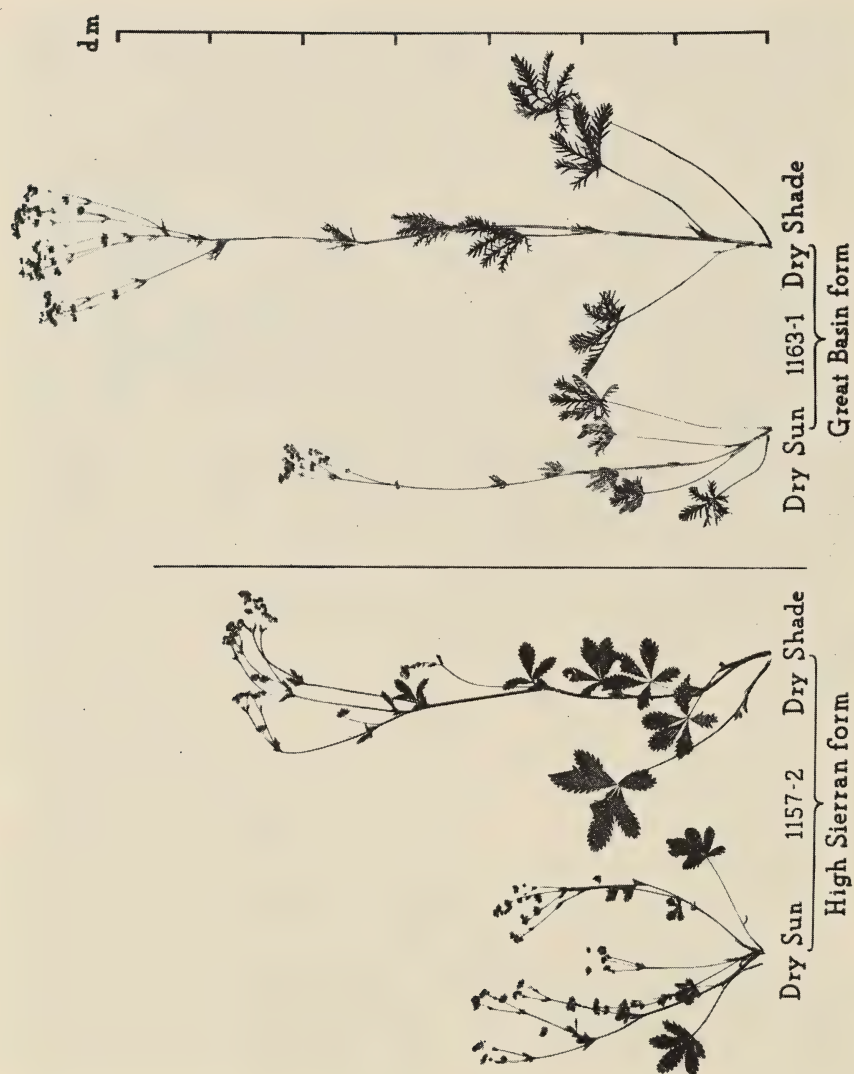


FIG. 63. Effect of sun and shade on clones of *Potentilla gracilis* ssp. *Nuttallii* (left) and *P. flabelliformis* (right) in the water-light gardens at Mather.

Plant 1157-2, dug September 13, 1926, at Tuolumne Meadows, Yosemite Park, at 2750 m. Plant 1163-1, dug August 20, 1925, at Wells, Elko County, Nevada, at 1710 m. Propagules of each planted in dry sun in 1927, in dry shade in 1933. The specimens were taken in 1935.

three of the alpine ecotype, and from one plant of *P. flabelliformis*. These forms do not react alike, but maintain their characteristic differences in all four environments, as is shown in the graphs of stem lengths (fig. 64) and flowering dates (fig. 65). In these graphs a

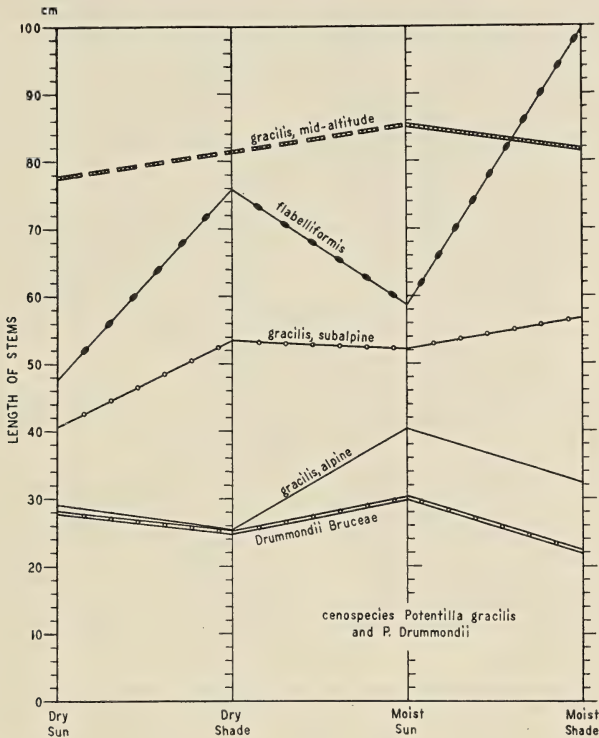


FIG. 64. Modifications in length of stems in clones representing ecotypes and ecospecies of the *Potentilla gracilis* complex and *P. Drummondii* ssp. *Bruceae* in the water-light gardens at Mather.

Graphs constructed from data averaged from the years 1934 to 1937. The groups are represented by mean values from two or three clones, except *P. Drummondii Bruceae*, of which there were six.

curve has been added for six plants of *P. Drummondii* ssp. *Bruceae*, a member of a related cenospecies that is taken up in detail in the next chapter.

The mid-altitude ecotype of *P. gracilis*, from Mather, has done so poorly in dry shade that three repeated attempts failed to establish it there; this ecotype succeeds best and about equally well in the two sun gardens. The subalpine ecotype, originally from Tuolumne Meadows, is fairly indifferent to differences in light and moisture.

It grows best in the moist shade, most poorly in the dry sun. The alpine ecotype likewise shows little preference, but is most vigorous in the moist sun and tends to remain as a rosette except in that garden. The single plant of *Potentilla flabelliformis* is definitely superior in the moist shade and thrives better in the shade than in the sun, but it does well under all conditions.

As in *P. glandulosa*, varied amounts of light and moisture have very little influence on the time of flowering in these plants except for a slight delay in the moist gardens, especially in moist shade (fig. 65). This lack of response is the more interesting in view of the very pronounced differences in earliness brought forth by the unlike

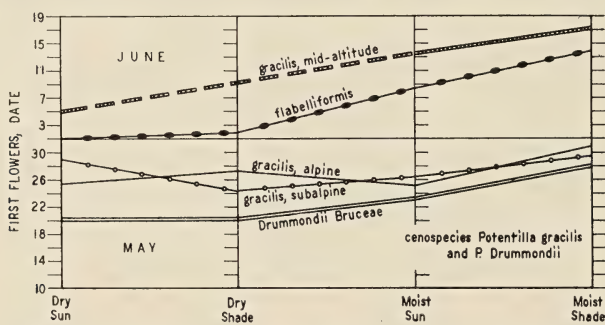
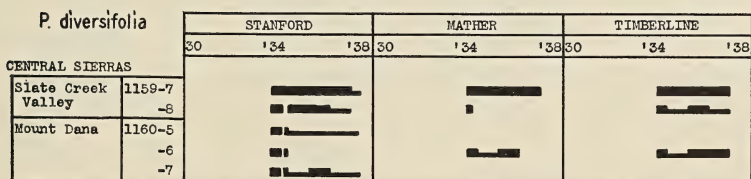
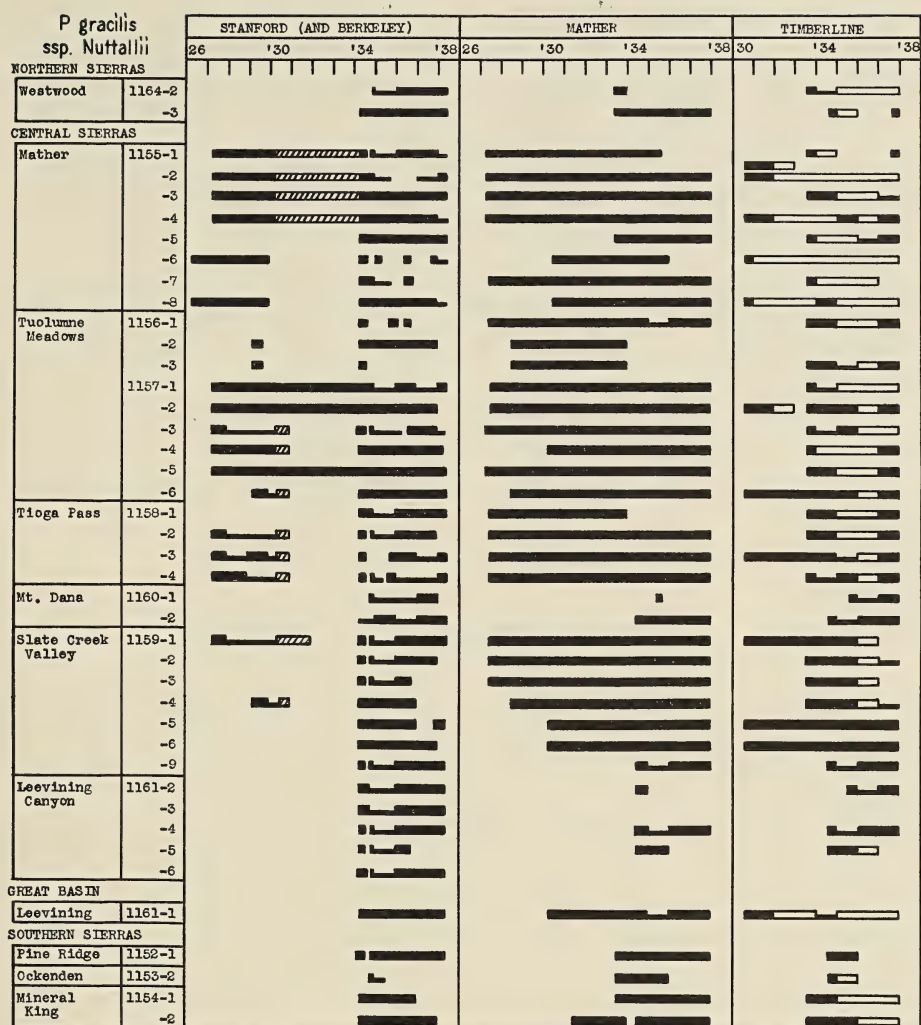


FIG. 65. Modifications in earliness in clones of the same groups shown in figure 64 in the water-light gardens. Data from the same sources as in figure 64.

climates of the three stations. It follows that the larger climatic differences are far more important in affecting earliness than are local environmental factors.

At present there do not seem to be consistent differences in vigor among different ecotypes and ecospecies of this complex in the water-light series of gardens that can be related to any ability to inhabit certain kinds of environments, as were pronounced in the case of *P. glandulosa*.

SURVIVAL, FLOWERING, AND RIPENING OF SEED. In comparing the survival of members of cenospecies *Potentilla gracilis* with that of *P. glandulosa*, it is to be noted that whereas several ecotypes of *glandulosa* were unable to survive at Timberline, all forms of the *gracilis* complex continue fairly well there. The records of their survival at the three stations are given in figures 66 and 67. Several plants from mid-altitude have been able to live at the alpine station for more than



■ maturing fruit □ flowering only — non-flowering

FIG. 66. Record of survival and flowering of clones of *Potentilla gracilis* ssp. *Nuttallii* and *P. diversifolia* at three altitudes. See table 17 for additional data on these plants. Shaded line indicates that the plant was kept in the Stanford lathhouse. The scale indicates years.

seven years, although they have almost never been able to produce ripe seed. The unfitness of the mid-altitude and subalpine ecotypes of this and its allied species for the alpine climate is therefore expressed less in lack of survival than in inability to produce ripe seed. In a late year such as 1936 this is especially evident, but in that particular year half of the transplants from the native Timberline population were also unable to mature seed. This, of course,

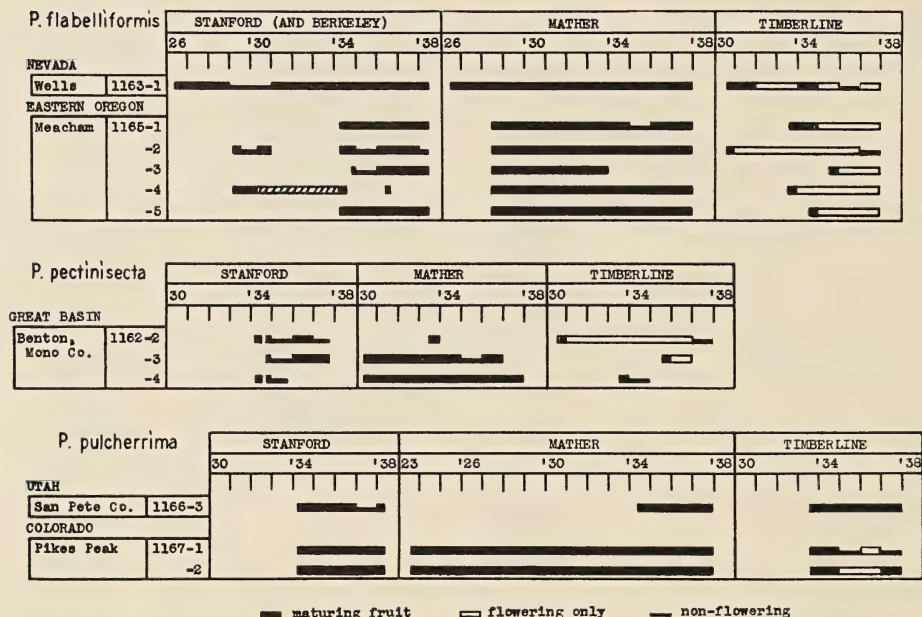


FIG. 67. Record of survival and flowering of clones of *Potentilla flabelliformis*, *P. pectinisetia*, and *P. pulcherrima* at three altitudes. See table 17 for additional data on these plants. The scale indicates years.

is not serious for a perennial plant. In fact, many plants native in an alpine habitat do not show a perfect adaptation to that environment, but they are nevertheless able to hold their own. *Potentilla diversifolia*, in contrast even to many of the alpine forms of *gracilis*, appears to be in perfect harmony with the climate in its native environs.

At Mather, survival, flowering, and maturing of fruit have been consistently satisfactory in all species, except that *P. diversifolia* and *P. pectinisetia* are difficult to establish and grow rather poorly. At Stanford most forms succeed fairly well. The numerous deaths recorded there in 1934 were due to an experimental location of the

Potentillas under the protection of oak trees. When it was noticed that the plants failed to establish themselves, that temporary location was abandoned later in the year, but many plants were lost in the interim.

At Stanford there has been some tendency for alpine plants not to flower. In *gracilis* this is evident in the plants from Tioga Pass and Mount Dana, and to a less extent in those native in Slate Creek Valley and the upper part of Leevining Canyon. *Potentilla diversifolia* flowers especially poorly. Its representatives are very weak each spring, but manage to regain some vigor by early summer, which is lost again before the following spring. In spite of this they may continue for several years, although they rarely attempt to flower. The only species that survives poorly at Stanford is *P. pectinisecta*, in spite of the fact that it produces more thrifty stems there than in its native Great Basin environment.

CYTOLOGY

It has already been mentioned that the chromosomal behavior in members of the cenospecies *Potentilla gracilis* is like that of apomictic species, but that field evidence indicates that sexual reproduction is also probable. Exact counts of the chromosomes of this group are very difficult to make because meiotic divisions are so irregular. It is not always possible to determine with certainty, for example, whether a chromosomal body in first metaphase is a true pair, or a univalent which is splitting. Most of the univalents, however, are scattered over the spindle and around the periphery of the equatorial plate. Also, the chromosomes are small, usually less than one micron in diameter in meiosis. This increases the difficulty of distinguishing between pairs and singles when they are observed in polar view.

Although the somatic plates in roots are fairly clear, the chromosomes are not well scattered, and in a plate with more than one hundred small chromosomes there are always two or three of uncertain identity. Accordingly, it is difficult to determine with certainty whether or not only numbers in the polyploid series are represented (i.e., 42, 49, 56, 63, 70, 77, 84, 91, 98, 105, etc.). There seems to be a tendency, however, for the chromosome numbers of the plants counted to range in the vicinity of these multiples, especially the even ones. The many chromosomes prevent expectation from interfering with the result, because the number is not known before all

chromosomes have been sketched and counted. Somatic divisions in the floral region have sometimes been used for supporting evidence. Some of these are very good, while others are inferior to those in good roots. A technical difficulty is presented in *Potentilla* by the many stiff hairs in the inflorescence that shred the paraffin ribbon during cutting and prevent it from sticking securely to the slide. Finally, some forms, especially those from the Great Basin, do not stain well. With such materials we find it helps to mordant the slides over night in a 1 per cent aqueous solution of chromic acid, followed by a brief rinsing in water before staining with crystal violet.

In the following, a brief tabulation of the chromosome counts in the cenospecies *Potentilla gracilis* will be given with some remarks on the chromosome behavior. Some of the somatic counts were made by Miss Ravage.

Potentilla gracilis Nuttallii:

Mid-altitude ecotype from Mather:

1155-2: $2n = 84-87$ (meiotic); 24 to 31 univalents, some of which become detached; $43 + 43$ counted in a second metaphase; formation of pollen abnormal: 34 monads, 17 tetrads and pentads, and one hexad were observed in one pollen sac in the tetrad stage; pollen size very irregular with many dwarf grains.

1155-3: $2n = ca. 109$ (roots).

1155-4: $2n = ca. 103$ (roots).

1155-5: $2n = 63$ (roots); (1155-5 and -6 are the two dwarf plants of this population.)

1155-6: $2n = 62$ (roots).

1155-7: $2n = ca. 101$ (roots).

1155-8: $2n = ca. 109$ (roots).

Subalpine ecotype from Tuolumne Meadows:

1157-1: $2n = ca. 68$ (roots).

1157-2: $2n = ca. 70$ (roots).

1157-4: $2n = ca. 66-74$ (roots).

1157-5: $2n = ca. 57$ (meiotic); $20_{II} + 17_I +$ a fragment observed in first metaphase; splitting of some univalents in anaphase; $31 + 35 (= 66)$ chromosomes $+ 2$ fragments observed in second metaphase; cells of pollen tetrads unequal in size and varying in number.

1157-6: $2n = ca. 59$ (mitotic), $ca. 54-55$ (meiotic); 21 to 28 univalents; splitting of univalents in anaphase; 37 chromosomes observed in second metaphase.

Alpine ecotype from Tioga Pass, Slate Creek Valley, and Upper Leevining Canyon:

1158-3: $2n = ca. 58$ (mitotic in floral region).

1159-1: $2n = ca. 84$ (roots).

1159-2: $2n = ca. 70$ (roots).

1159-5: $2n = ca. 64$ (roots); the margin of uncertainty is only 1 or 2 chromosomes.

1159-6: $2n = ca. 59$ (mitotic, floral region), $ca. 58$ (meiotic); 22 to 29 univalents, some of which split in anaphase; pollen size very variable, some pollen empty.

1159-9: $2n = ca. 70$ (roots).

1161-4: $2n = ca. 54$ (mitotic in floral region).

Great Basin form from Leevining, elevation 1980 m.:

1161-1: $2n = ca. 80$ (roots), $ca. 79-80$ (mitotic in floral region).

Northern Sierra Nevada near Westwood:

1164-3: $2n = ca. 78$ (roots).

1164-5: $2n = ca. 56$ (mitotic in roots), $ca. 51 + 4$ fragments (meiotic); 9 to 10 univalents; pollen plentiful and fairly regular in size.

1164-6: $2n = ca. 52$ (roots).

Wasatch Mountains, near Park City, Summit Co., Utah, elevation 2000 m.:

1166-2: $2n = ca. 72$ (roots).

Potentilla diversifolia, Slate Creek Valley and Mount Dana:

1159-7: $2n = ca. 101$ (roots); there is an abundance of apparently good pollen, although it is slightly variable in size with some dwarf grains.

1159-8: $n = 41-42$ in second meiotic metaphase; the pollen tetrads appear fairly regular.

1160-6: $2n = ca. 90-91$ (meiotic); 11 to 12 univalents, some quadrivalents and trivalents; pollen tetrads fairly regular.

It is very probable that the reproduction of *P. diversifolia* is primarily sexual.

Potentilla pectinisecta from Benton, Mono County:

1162-1: $n = 21$ (diaphase); chromosomes regularly paired.

1162-4: $n = 21$ (first metaphase); chromosomes regularly paired.

Potentilla flabelliformis from Wells, Nevada, and Meacham, Oregon:

1163-1: $2n = ca. 60-65$ (roots), $ca. 56$ (first metaphase of meiosis); 11 to 14 univalents, occasional quadrivalents and trivalents; $31 + 35 = 66$ counted in second metaphase; a great variation in pollen size.

1165-3: $2n = ca. 64$ (mitotic in floral region); 10 to 18 univalents.

1165-4: $2n = ca. 62$ (mitotic in floral region).

Hybrids of *P. flabelliformis* \times *P. gracilis Nuttallii* from Meacham, Ore.:

1165-2: $2n = ca. 62-65$ (roots); $ca. 8$ to 16 univalents in first metaphase.

1165-5: $2n = 61-62$ (mitotic in floral region); 11 to 17 univalents in first metaphase.

Potentilla pulcherrima from Wasatch Mountains, Utah, and Pikes Peak, Colorado:

1166-3: $2n = ca. 70$ in second meiotic metaphase, varying between $n = 33$ and 35; pairing fair, with only 4 to 6 univalents; pollen very good and plentiful, with only a few dwarf grains; this probably reproduces sexually.

1167-1: $2n = ca. 108$ (mitotic in floral region); $ca. 57$ and 59 counted in

different second meiotic metaphases; apparently much good pollen with only a few dwarf grains. The pollen mother cells dissolve in some anthers in prophase.

1167-2: $2n = ca. 71$ (meiotic); 13 to 17 univalents in first meiotic metaphase, while the others were bivalents.

Shimotomai (1930) reported $2n=70$ for both *Potentilla gracilis* and *P. flabelliformis*, but Popoff (1935) found $2n=84$ for *gracilis*. Both authors obtained most of their material from botanical gardens. This discrepancy in the determination of *gracilis* can now be well understood.

Intraspecific variations in chromosome numbers similar to these of the *Potentilla gracilis* complex were observed in *Festuca ovina* by Turesson (1930b, 1931a) and in *Poa pratensis* by Müntzing (1933). Other apomictic complexes that have been cytologically investigated with reference to their taxonomy and distribution are *Antennaria* (Stebbins, 1932a, 1932b), *Crepis* (Babcock and Stebbins, 1938), *Taraxacum* (Gustafsson, 1932, 1937), and *Rubus* (Gustafsson, 1939).

Although *Potentilla gracilis* shows variation in chromosome number within the populations, there is some indication that the forms with the highest numbers (nona- to 16-ploid) are found at lower elevations, whereas mainly octoploid to nonaploid plants have been found in the subalpine and alpine populations.

The following tabulation, taken from a series of plants from Mather, shows their chromosome numbers and modifications in size and earliness at Mather and Timberline. The two plants with the fewest chromosomes have shorter stems at Mather than the others, but at Timberline they exceed some of the plants with many chromosomes. In this reaction they resemble the subalpines from Tuolumne Meadows which have equally low chromosome numbers.

PLANT NUMBER	$2n$	LONGEST STEM (CM.)		DATE OF FIRST FLOWERS	
		Mather	Timberline	Mather	Timberline
1155-2 (tall, late).....	ca. 84-87	85.7	23.3	June 13	Aug. 28
-3 (tall, late).....	ca. 109	90.0	21.5	June 12	Sep. 1
-4 (tall, late).....	ca. 103	77.5	23.0	June 12	Aug. 24
-7 (tall, late).....	ca. 101	88.5	39.0	June 13	Sep. 7
-8 (tall, late).....	ca. 109	78.3	39.3	June 9	Sep. 12
-5 (short, early).....	63	64.0	38.0	June 1	Aug. 10
-6 (short, late).....	62	40.0	35.0	June 18	Sep. 2

The majority of plants at Mather are tall, late flowering, and have high chromosome numbers (12- to about 15-ploid), but the last two in the above tabulation are nonaploid. One of them is also early like the subalpine, but the other is late like the mid-altitude plants.

IV

POTENTILLA DRUMMONDII AND POTENTILLA BREWERI

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Potentilla Drummondii Lehm. and *P. Breweri* S. Wats. are species of a strictly subalpine and alpine distribution that are included in a group considerably smaller in size than either the *gracilis* or the *glandulosa* complex. Judging from strong circumstantial evidence, both are probably members of one cenospecies. They are found from the southern Sierra Nevada, in California, northward to the Rocky Mountains of British Columbia. Certain elements from the Rocky Mountains of Wyoming, Colorado, and Utah probably should also be included here. Both *Drummondii* and *Breweri* extend their ranges to slightly higher altitudes than the alpine *P. diversifolia* of the *gracilis* complex, i.e., to about 3650 meters.

The members of this group differ from those of the cenospecies *P. gracilis* in having pinnate leaves, but students of the genus, such as Wolf and Rydberg, have disagreed widely as to where to place them, both in relation to each other and in relation to members of cenospecies *gracilis*. We place them next to the *gracilis* complex, for there is an evident morphological transition between *P. diversifolia* and *P. Drummondii*, and the cytological situation is similar in the two groups. Chromosome numbers of both *Drummondii* and *Breweri* range between $2n=ca. 64$ and $ca. 105$. In both, many univalents are seen in first metaphase of meiosis, the pollen is irregular in size, and plants of the individual population differ in their number of chromosomes.

TAXONOMY

Potentilla Drummondii and *P. Breweri* are thought to be members of one cenospecies because they are morphologically and cytologically similar, and, where they meet, intermediates are found that suggest hybridization and recombination. This cenospecies would take the oldest name, *Drummondii*. Our experimental studies have been



FIG. 68. Races of the cenospecies *Potentilla Drummondii* from different elevations as grown in a uniform garden at Mather.

Left (1168-3), *P. Drummondii* ssp. *typica*, dug July 12, 1931; center (1169-1), *P. Drummondii* ssp. *Bruceae*, dug September 14, 1926, $2n = ca. 64$; right (1172-3), *P. Breweri*, dug August 1, 1933, $2n = ca. 100$. The specimens were all taken in 1935.

concerned with the Pacific Coast representatives of this group only, but further investigation would doubtless show that certain scarcely distinguishable forms of the Rocky Mountains of Wyoming and Colorado, and of the Uintas of Utah, belong likewise in this cenospecies.

The flower structure is remarkably uniform in these species, and is similar in details to that of *P. diversifolia*. The best diagnostic characters are in the leaves. Three natural units can be distinguished in *Drummondii* and *Breweri*; these are shown in figure 68. The forms of the illustration were taken along the transect of the transplant stations: the plant from White Wolf is *P. Drummondii* ssp. *typica*; that from Tuolumne Meadows is *P. Drummondii* ssp. *Bruceae*; and the one from Timberline is *P. Breweri*. Details of their differences in foliage can be seen more clearly in figure 70.

The three units may be keyed out as follows:

- Leaflets dark green, almost glabrate or slightly to moderately strigose, more densely pilose when young, 2 to 5 pairs, moderately spaced, mostly large, 20 to 60 mm. long, usually quite irregular in size, cuneate-obovate; leaf blade narrowly ovate-oblong in outline.....1a. *P. Drummondii* ssp. *typica*
- Leaflets gray-green, densely villous or pilose, sometimes \pm tomentose, especially when young, 2 to 4 pairs, closely approximate, 15 to 35 mm. long, irregular in size, broadly obovate, the basal pair usually divided to base; leaf blade orbicular-ovate in outline.....1b. *P. Drummondii* ssp. *Bruceae*
- Leaflets white with a dense tomentum, at least when young, sometimes quite green in age, 4 to 6 pairs, usually crowded, small, 10 to 25 mm. long, quite regular in size, broadly flabelliform, several pairs often divided to base; leaf blade lance-oblong in outline.....2. *P. Breweri*

1. *POTENTILLA DRUMMONDII* Lehm., Stirp. Pug. 2:9, 1830

Figure 69

1a. *Potentilla Drummondii* Lehm. ssp. *typica* Keck nom. nov.

Figures 68 (1168-3) and 70

Potentilla Drummondii Lehm., loc. cit.

Potentilla dissecta var. *Drummondii* Kurtz, Bot. Jahrb. 19:374, 1894.

Potentilla cascadiensis Rydb., Mem. Dept. Bot. Columbia Univ. 2:109, 1898.

Type, from Chiquash Mountains, Skamania County, Washington, *Suksdorf* 2165, seen at New York. A form with short leaflets, but neither morphologically nor geographically a distinct unit.

Potentilla Drummondii var. *genuina* Wolf, Bibl. Bot. 16(71):492, 1908.

Potentilla Drummondii var. *cascadiensis* Wolf, *ibid.*

Potentilla anomalofolia Peck, Proc. Biol. Soc. Wash. 49:110, 1936. The type collection, from three miles north of Klamath Agency, Oregon, *Peck* 16819, has been seen at the University of California. A robust form.

Subalpine and alpine situations, often in wet ground, from the Rocky Mountains of central British Columbia and adjacent Alberta, southward through the high mountains of Washington and Oregon to Humboldt and Tulare counties, California.

Subspecies *typica* varies considerably as to the size and cut of the leaflets. In Canadian material the leaflets are usually large and only moderately cut; in California they are sometimes deeply cut and small, but there are exceptions to both trends. We have been unable to discover any natural subunits based on this variation. *Potentilla Drummondii* is essentially a rare species, and because of the un-

doubted presence of apomixis in it, there are ample opportunities for local isolation and differentiation. We have seen herbarium material from Rocky Mountain Park, Alberta, that appears to be transitional to *P. diversifolia*.



FIG. 69. Distribution of *Potentilla Breweri* and *P. Drummondii*, as determined from collections in various herbaria.

In the central Sierra Nevada this subspecies descends to somewhat lower elevations than either of the following units, but it does not occur below the Canadian life zone, and its rare occurrence there tends to minimize the significance of this observation.

1b. **Potentilla Drummondii** Lehm. ssp. **Bruceae** (Rydb.) Keck
comb. nov.

Figures 68 (1169-1) and 70

Potentilla Bruceae Rydb., N. Amer. Fl. 22:342, 1908.

In situations similar to those of ssp. *typica*, from Lake County, Oregon, southward through the Sierra Nevada to Tulare County, California, at elevations of 2100 to 3250 m. Type, from Warner Mountains, Oregon, *Bruce 2301*, seen at New York.

Transitions between this subspecies and *typica* are frequent, although either subspecies in pure stands looks sufficiently distinct. There are also transitions between this subspecies and *P. Breweri*. All three of these units may be found together in many Sierran alpine meadows.

2. **POTENTILLA BREWERI** S. Wats., Proc. Amer. Acad. 8:555, 1873

Figures 68 (1172-3), 69, and 70

Potentilla Breweri var. *expansa* S. Wats., in Brew. & Wats., Bot. Calif. 1:179, 1876. Type, from Sierra County, California, taken by J. G. Lemmon, seen at Gray Herbarium. The form with loosely expanded, instead of congested, cymes; a character, to some extent at least, partially dependent upon age.

Potentilla plattensis var. *leucophylla* Greene, Erythea 1:5, 1893. The type came from Independence Lake, Nevada County, California, and was taken June 26, 1892, by C. F. Sonne. An isotype has been seen at the University of California. This is the usual form, with expanded cyme.

Potentilla versicolor Rydb., N. Amer. Fl. 22:344, 1908. Type, from Gearhart ("Grayheart") Butte, Lake County, Oregon, *Coville & Leiberg 307*, seen at U. S. National Herbarium. In this the leaflets are small and rather well separated.

Principally in alpine meadows, from the Cascade Range and Steens Mountains, of Lane and Harney counties, Oregon, southward through the Sierra Nevada to Tulare County, California, at elevations of 1600 to 3650 m. Type, from the summit of Mono Pass, California, seen at Gray Herbarium.

Wolf, in his Monograph (1908), separated this from *P. Drummondii* by 290 pages, for he placed them in different series on the basis of presence or absence of true tomentum. The artificiality of such a separation is evident from a close study of the members of this group, because different individuals of *P. Drummondii Bruceae* from the same locality may have or may lack tomentum. This

character is one that is affected by the age of the part, for young leaves and petioles are ordinarily much more pubescent in all three of these units than old ones.

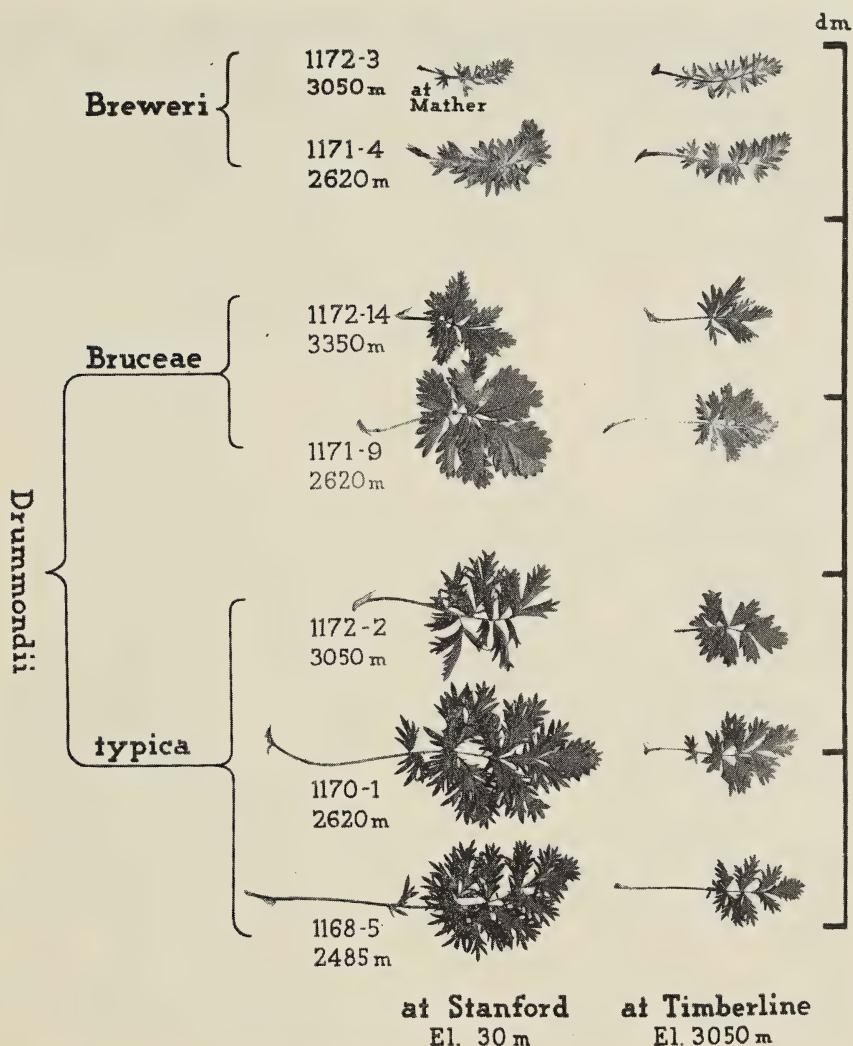


FIG. 70. Leaves of clones representing races of the *Potentilla Drummondii* complex at Stanford and Timberline.

Altitudes of the original habitats of the individuals represented are indicated; further information is given in table 18. The specimens were taken mostly in 1936 and 1937, and represent typical hereditary variations (in the vertical comparisons) and modifications (in the horizontal comparisons).

BEHAVIOR IN THE VARIED-ENVIRONMENT EXPERIMENTS

The cenospecies *Potentilla Drummondii* is quite variable in the central Sierra Nevada, and, in addition, all three taxonomic units may be found growing together at one locality. The leaves marked 2620 m. in figure 70 all came from plants originally taken in Tuolumne Meadows and represent the three taxonomic units. Moreover, the populations at this locality are so variable that morphological counterparts of all the plants in this figure could be found there. Several points are illustrated by the basal leaves. First, they show the more obvious taxonomic differences between the three units, *P. Breweri* and the two subspecies of *P. Drummondii*; secondly, they represent a minor sample of the variation along the transplant transect within these units; and in the third place, they show the Stanford and Timberline modifications of the individual clones. It is evident within each unit that the plants from the higher elevations have the smaller leaves. This represents a general trend in the wild, and plants with the smallest leaves are also the most dwarfed in stature.

When the plants of which leaves are shown in figure 70 are transplanted from Stanford to Timberline, every one will change, but to a different degree. There is a tendency for all to become similar in size, although the characteristic distinctions between the units remain. *Potentilla Breweri* and the alpine races of *P. Drummondii* are less modifiable than the subalpine plants. This figure also shows that morphologically *Bruceae* belongs with *Drummondii* rather than with *Breweri*, where, unfortunately, it has been left most frequently by botanists.

POTENTILLA DRUMMONDII. The various members of *Potentilla Drummondii* react differently to the environments at the transplant stations. This may be observed both from figure 71 and from table 18. From their reactions, plants of *Drummondii* in these experiments may be divided into three groups: subalpine ssp. *typica*, subalpine ssp. *Bruceae*, and the alpine races of both subspecies, which appear to constitute a third ecological unit in the species. The evidence on the last unit, however, is very scarce, because these plants are very difficult to retain in culture. This fact, in itself, is an additional indication that the alpine forms are different from the subalpine.



FIG. 71. Modifications at three altitudes in clones representing three races of *Potentilla Drummondii* from the station transect.

Below (1168-3): ssp. *typica* dug July 12, 1931, at White Wolf, at 2485 m.; the propagule at Mather was planted in 1931; those at Stanford and Timberline were taken from it and planted in 1934. *Center* (1171-9): a subalpine form of ssp. *Bruceae*, dug August 4, 1927, at Tuolumne Meadows, at 2620 m.; the propagule at Mather was planted in 1928; those at Stanford and Timberline were taken from it and planted in 1934 and 1933 respectively. *Above* (1172-14): an alpine form of ssp. *Bruceae*, dug August 20, 1933, on Mount Dana, at 3350 m.; the propagules at all stations were planted in 1934. All specimens taken in 1936.

TABLE 18
MODIFICATIONS IN LENGTH AND NUMBER OF STEMS AND EARLINESS IN CENOSPECIES POTENTILLA DRUMMONDII
(Data from years from 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
P. DRUMMONDII TYPICA, SUBALPINE: 1168-2, White Wolf, Tuolumne Co., 2485 m. -3, Same..... -4, Same..... -5, Same..... 1170-1, Tuolumne Meadows, 2620 m.....	56.0 61.0 45.0 53.5 58.5	44.0 49.0 46.0 48 46.5	28 38.5 28 26.0 25.5	27.5 8.0 12.5 17.5 7.0	15.5 10.5 10.5 30 10.5	7 6.0 5 4.5 3.0	Apr. 13 Apr. 17 Apr. 20 Apr. 17 Apr. 28	May 17 May 20 May 21 May 16 May 20	Jul. 23 Jul. 29 Aug. 5 Jul. 31 Jul. 31
Means..... Mean differences..... t=.....	54.8±2.76 St—Ma:8.10±2.60; Ma—Ti:17.50±2.09 3.116	46.7±0.87 Ma—Ti:17.50±2.09 8.362	29.2±2.38	14.5 St—Ma:0.90±5.63; Ma—Ti:10.30±3.86 0.016	15.4 5.1	5.1 2.663	Apr. 19.0	May 18.8	Jul. 30.0
P. DRUMMONDII BRUCEAE, SUBALPINE: 1169-2, Tuolumne Meadows, 2620 m..... -3, Same..... -4, Same..... -5, Same..... 1171-1, Same..... -6, Same..... -7, Same..... -8, Same..... -9, Same..... -10, Same.....	12 25 15 22 23 38 23.5 26 33.0 27	31.3 35.0 39.0 30.0 20.5 41.7 38.0 31.3 35.7 35.7	29.7 33.3 30.3 32.3 27.5 37.7 37.3 20.0 32.7 22.7	2 7 1 4 2 8 1.0 2 7.5 2	6.3 18.3 14.3 20.0 2.0 18.0 15.3 21.0 20.0 27.7	18.3 25.0 12.0 21.5 17.5 30.3 40.0 4.3 19.3 3.7 May 3 May 1 May 1 May 1 Apr. 28 May 8 Apr. 25 Apr. 27 May 1	May 24 May 22 May 24 May 22 May 19 May 22 May 22 May 20 May 20 May 20	Aug. 1 Aug. 1 Jul. 31 Jul. 27 Jul. 20 Jul. 23 Jul. 26 Jul. 25 Jul. 25 Aug. 6
Means..... Mean differences..... t=..... Differences, typica minus Bruceae..... t=.....	24.5±2.18 Ma—St:9.37±2.06; Ma—Ti:3.47±1.94 4.550 30.3±3.52 8.60	33.8±1.89 Ma—Ti:3.47±1.94 1.710 12.9±2.08 6.18	30.4±1.81	3.7 Ma—St:12.64±2.26; Ti—Ma:2.90±4.07 5.590 10.8	16.3 0.714 -0.9	19.2 0.714 -14.1	Apr. 30.6	May 21.5	Jul. 27.8 -11.6 days -2.7 days 2.2 days

(Continued on following page)

TABLE 18—Continued

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
P. DRUMMONDII, ALPINE RACES:									
<i>Ssp. typica:</i>									
1172-1, Slate Creek, 3050 m.....	13	5	Mar. 15
-2, Same.....	15.5	28.5	2.5	5.5	Mar. 30	Jul. 25
<i>Ssp. Bruceae:</i>									
1172-12, Mt. Dana, 3350 m.....	14	26.0	2	22.5	May 12	Jul. 22
-14, Same.....	12	23	22.0	4	1	17.0	Mar. 19	May 18	Jul. 21
Means.....	13.5	18.5	25.5	3.8	1.5	14.7	Mar. 21.3	May 15.0	Jul. 22.7
P. BREWERI:									
1171-2, Tuolumne Meadows, 2620 m.....	27.3	22.3	Jul. 20
-3, Same.....	31.5	16	24	11.5	1	35	Apr. 5	Jul. 23
-4, Same.....	22.5	15	31.7	2.0	3	21.3	Apr. 16	May 18	Jul. 22
-5, Same.....	28.0	29.0	Jul. 22
1172-3, Slate Creek, 3050 m.....	16	23.0	2	9.5	May 22	Jul. 20
-4, Same.....	16.5	24.0	6.5	18.0	May 13	Jul. 21
Means.....	27.0	15.9	26.3	6.8	3.1	22.5	Apr. 10.5	May 17.7	Jul. 21.3

The reaction of subalpine *P. Drummondii typica* is remarkable for an ecotype from this elevation, and is very different from any in *P. glandulosa* or the *gracilis* complex. Figure 71 (1168-3) shows that it produces longer stems at Stanford than at Mather, and table 18 indicates that this difference is statistically significant for the sample tested. Furthermore, its plants produce almost as many stems per propagule at Stanford as at Mather. This is more than the Coast Range ecotype of *P. glandulosa* did, even though it is native in the hills surrounding Stanford.

The subalpine *P. Drummondii Bruceae* (fig. 71, 1171-9) has quite the reverse reaction. At Mather as contrasted with Stanford there are significant increases in both the length and the number of stems. Why these two forms, belonging to the same species and found growing side by side in nature, should behave so differently when transplanted, is an interesting question. The results show how different their metabolism must be. Possibly an explanation lies in the suggestion that the origins of these subspecies differ. Morphologically, ssp. *Bruceae* is somewhat intermediate between ssp. *typica* and *P. Breweri*, and it so happens that it occurs mainly within the same area as *Breweri*, whereas *typica* has a far wider distribution (fig. 69).

The alpine races of *P. Drummondii* are dwarf at all three stations (fig. 71, 1172-14). The three plants grown at Timberline produced more and longer stems there than elsewhere (table 18). Alpine races of the two subspecies are not very unlike, for the forms referred to *Bruceae* from the highest elevations are only moderately pubescent.

Modifications in earliness follow a new pattern in this species. All three ecotypes flower at almost the same time at either Mather or Timberline, with the alpine plants slightly the earliest (table 18). At Stanford, however, there is a remarkable difference of about forty days between the earliest and the latest. Here the alpine plants of both subspecies are approximately one month earlier than subalpine *typica*, which, in turn, is approximately twelve days earlier than subalpine *Bruceae*. The lateness of the latter is doubtless associated with its poor growth at Stanford, where it apparently is unable to build up sufficient reserves for abundant flowering. One or more years elapse before this form flowers after it is transplanted to Stanford, and it frequently lapses into a non-flowering state (fig. 76). At Timberline all three ecotypes flower early enough to produce ripe

seed every year, a fact which contrasts very markedly with the behavior of *P. gracilis* from the same altitudes.

All three ecotypes of *P. Drummondii* are therefore truly alpine in earliness. The only indication that the subalpine form of *typica* is really a subalpine ecotype is its reduced vigor at Timberline, as shown by the reduced number of stems. In this respect it reacts like a lowland form.

We are unable to determine whether *P. Drummondii* was a lowland species that was forced up the mountains by competition, or whether it has always been alpine and by chance is able to produce greater vigor in a lowland habitat than where it is native. It is of minor importance which of these alternatives is the more probable, for both are equally interesting and revealing as to the nature of a high-montane plant.

POTENTILLA BREWERI. The second species in this complex reacts differently from any of the three ecotypes of *P. Drummondii*, but like another high alpine species previously considered, *P. diversifolia*. As shown in figure 72, it is much smaller at Mather than at either Timberline or Stanford. It is definitely reduced in vigor when carried down the mountains from Timberline, as shown in table 18 by the marked reduction in the number of stems at Stanford and Mather as compared with Timberline. In fact it attains real success, both as to vigor and as to survival, only at the alpine station. Actually, twice as many propagules have been planted at both Stanford and Mather as at Timberline, but for the most part they died or did not flower, as is plainly evidenced by the gaps in this table.

At Mather and Timberline, *P. Breweri* is not significantly earlier than the three ecotypes of *Drummondii*. At Stanford, however, the two surviving plants from Tuolumne Meadows were nearly three weeks earlier than *Drummondii Bruceae* from the same locality, and more than a week earlier than subalpine *typica*.

Judging from the differences in their growth reactions at the transplant stations, *P. Breweri* and *P. Drummondii* evidently differ in their physiological characteristics. The former has a very limited altitudinal distribution, like *P. diversifolia*, which follows a similar pattern of reaction. The wider distribution of *Drummondii*, both horizontally and altitudinally, is perhaps due to the greater physiological adaptability of its subalpine ecotypes, particularly of *typica*,

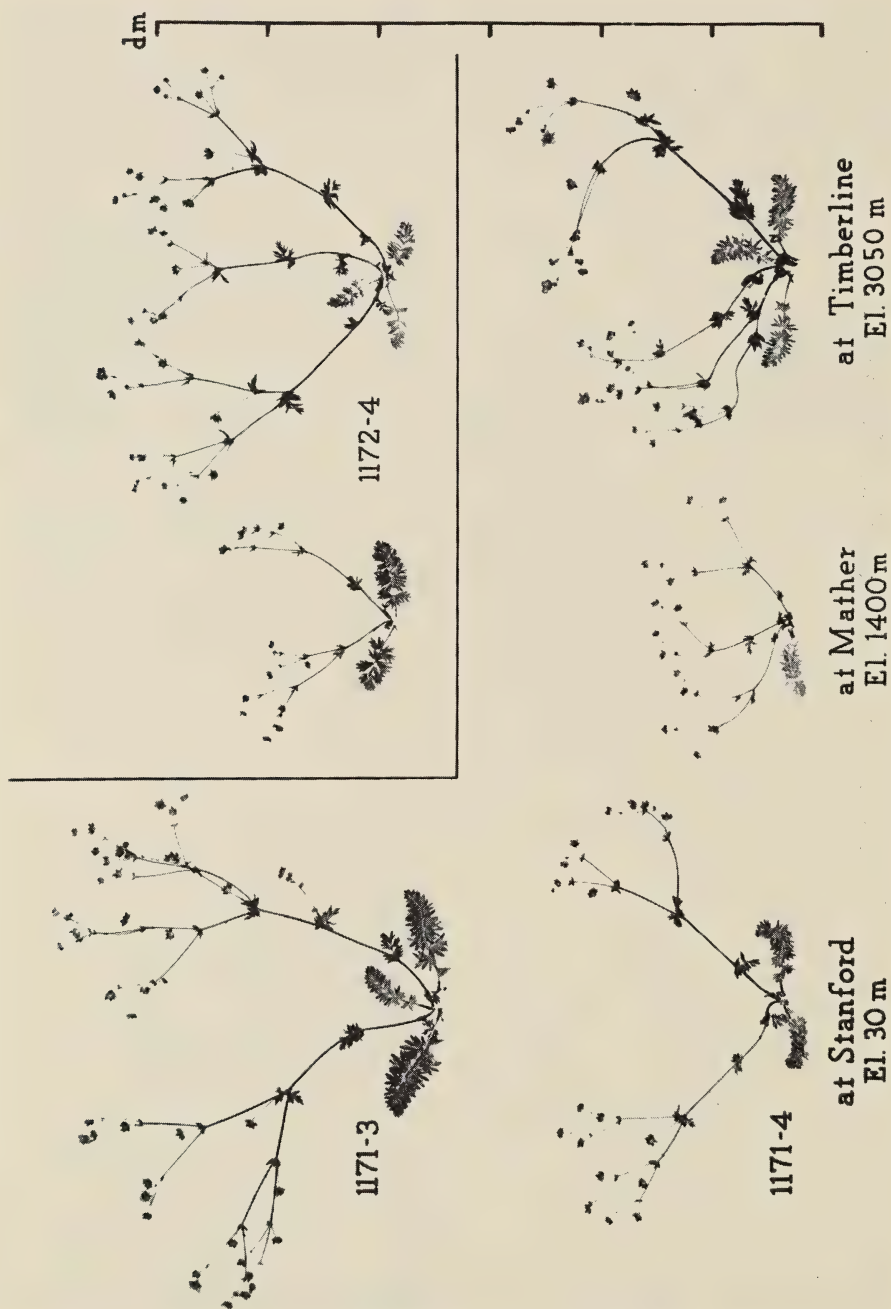


FIG. 72. Modifications in clones of *Potentilla Brewerii* at three altitudes.

Below (1171-4), dug August 4, 1927, at Tuolumne Meadows, at 2620 m.; the propagule at Mather was planted in 1928; divisions from it were planted at Stanford and Timberline in 1934 and 1930, respectively. The Mather specimen was taken in 1935, the others in 1936. Above: Left (1171-3), dug with 1171-4; planted at Stanford in 1934 as a division from a propagule held at Mather; specimen taken in 1937. Right (1172-4), dug August 1, 1933, at Timberline station; the propagules at Mather and Timberline were planted in 1934; the Mather specimen was taken in 1936, the Timberline one in 1937.

which can thrive at very different altitudes. But it is equally significant that *Drummondii* has produced three ecotypes instead of merely one, as has *Breweri*.

RESPONSE TO DIFFERENCES IN LIGHT AND MOISTURE. *Potentilla Drummondii* reacts to conditions in the water-light gardens at Mather like the alpine races of cenospecies *P. gracilis*. Reactions of six plants of *Drummondii Bruceae* in these gardens were shown in figures 64 and 65 under *gracilis*. Plants in shade have larger and thinner leaves, reduced pubescence, fewer stems, and fewer flowers per stem than plants in the sun. Also, vigor is usually reduced. The greatest success is achieved in the moist sun garden, and the least in dry shade. In some of the earlier "optimum" gardens, that were partly shaded by trees and amply supplied with moisture, basal leaves of *Drummondii Bruceae* became exceptionally large and an extra pair of leaflets were formed. At the same time, other leaves on the same division retained the normal number of pairs. Differences in light caused more pronounced modifications than differences in moisture, but in either case the modifications were relatively small. It was impossible to establish *P. Breweri* in this series of gardens because of its poor survival at Mather.

COMPARISON OF THE ECOTYPES AND THE ECOSPECIES

VIGOR AND EARLINESS. The behavior of the ecotypes and ecospecies of the *Drummondii* complex is summarized in a series of graphs. Figure 73 illustrates the contrasting modifications of subalpine *Drummondii typica* and alpine *Drummondii*. The former has the longest stems at Stanford and the shortest at Timberline, while the latter has just the opposite. Subalpine *Drummondii Bruceae* shows only slight differences at the three stations, but *Breweri* varies in having the shortest stems at the intermediate elevation, Mather.

Likewise, figure 74 shows that all four units bloom almost equally early at Mather and Timberline, but are well separated at Stanford. At Timberline all flower early enough to develop ripe seed every year. This would be true were they to follow the cadence of the alpine ecotypes of *P. glandulosa* and *P. gracilis*, but, as a matter of fact, they mature at a still more rapid rate than these. After their fruit is ripe at Timberline, time still remains for subsequent growth of basal leaves. At Mather *Drummondii* has a second well-defined flowering period after fruit has ripened on the first set of flowering

stems. At Berkeley and Stanford the more vigorous individuals sometimes develop successive inflorescences throughout the summer and fall, following maturation of the primary set of flowering stems.

The yearly fluctuations in earliness are not nearly so marked in this complex as in *Potentilla glandulosa* and *P. gracilis*. This may be seen in figure 75, showing the annual variations in earliness at Mather and Timberline. It is very evident from these graphs that members of the *Drummondii* complex were hardly delayed at all in their flowering at Timberline in the year 1936, nor conspicuously acceler-

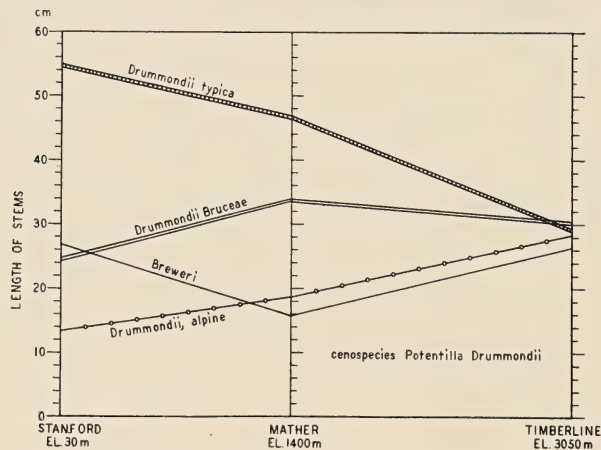


FIG. 73. Modifications in length of stems in clones of *Potentilla Drummondii* and *P. Breweri* grown at three altitudes.

The graphs are constructed from data averaged from the years 1935 to 1937, for the plants of the various groups indicated in table 18.

ated at Mather in the same year, as were *P. glandulosa* and most forms of *P. gracilis* (see figs. 30, 31 and 61, 62). It may also be seen from the Timberline graph that *P. Breweri* and the alpine *P. Drummondii* are consistently somewhat earlier than the subalpine ecotypes of *Drummondii*. This consistency in behavior probably means that the differences are significant, although they are not great.

As to hardiness, subalpine *Drummondii typica* is more frost-resistant than most forms of *P. gracilis*, but it is, nevertheless, the most susceptible form in its complex. The other forms of *Drummondii* are somewhat damaged by severe September frosts at Timberline, but are able to continue their activity. *Potentilla Breweri*, the most frost-resistant of the three, showed no injury at times when *Drummondii typica* was badly damaged.

SURVIVAL AND FLOWERING. All the ecotypes and ecospecies of this cenospecies survive well and produce ripe seed at Timberline regardless of whether they come from subalpine or alpine elevations. This rather unusual reaction is shown in the survival patterns of figure 76.

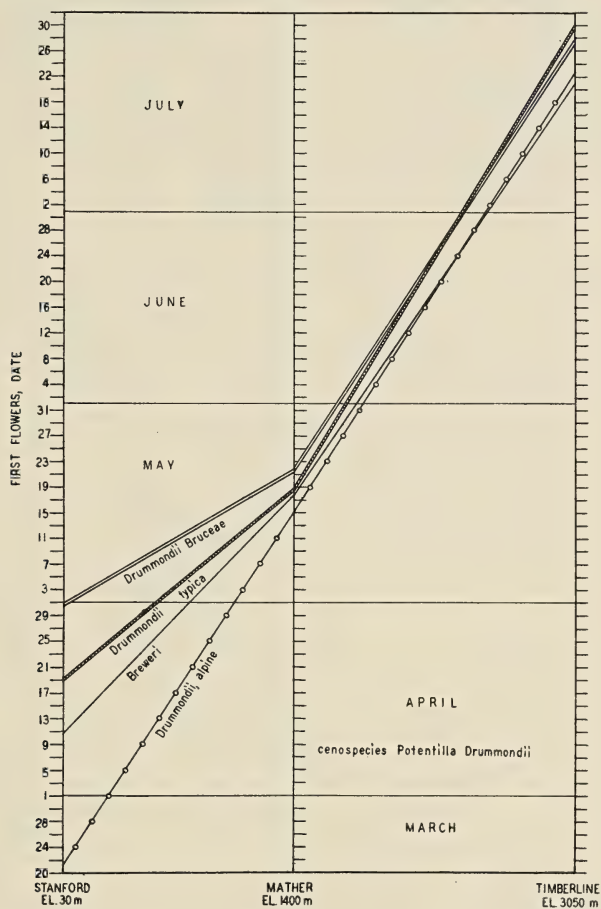


FIG. 74. Modifications in date of first flowers in clones of *Potentilla Drummondii* and *P. Breweri* grown at three altitudes. Data from same sources as in figure 73.

All forms of this cenospecies, with the possible exception of subalpine *Drummondii typica*, grow at Timberline as well as or better than at the other two stations. The chart shows that subalpine *Drummondii typica* succeeds well at Stanford too. The reduced flowering at Stanford is obvious in the other forms. Also, the poor survival of *Breweri* and alpine forms of *Drummondii* at Stanford and Mather is shown.

The differences in reactions that appear when these biological units of one cenospecies are tested in the transplant experiments indicate that these units are physiologically very dissimilar. The nature of

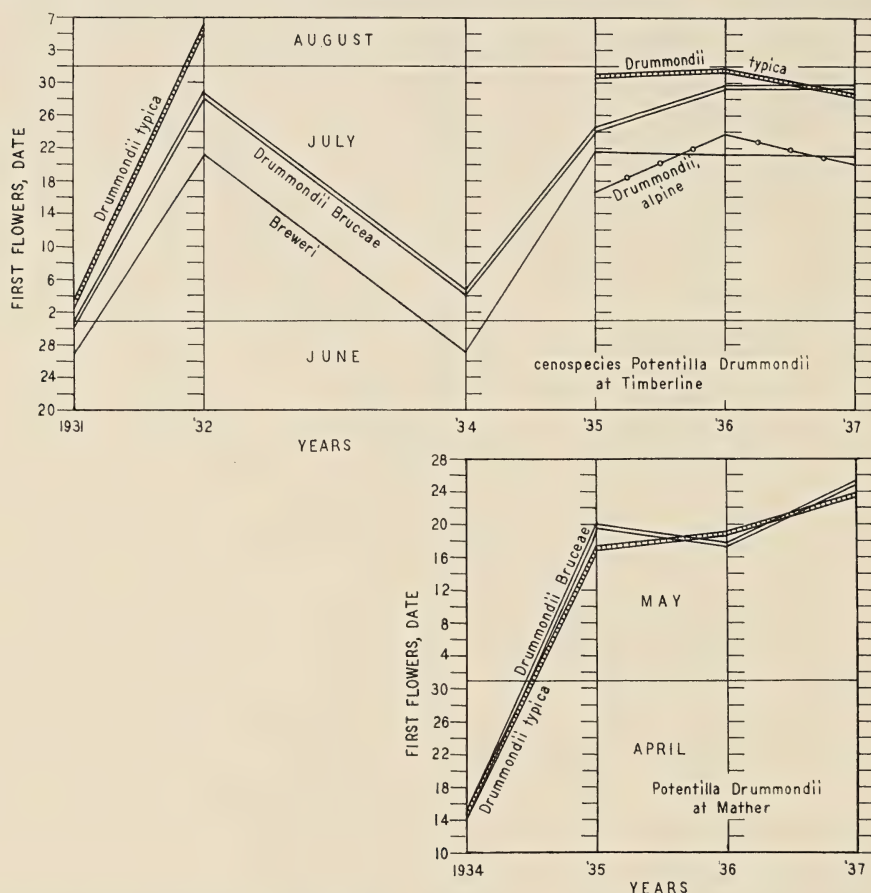


FIG. 75. Yearly variation in the dates of first flowers at Timberline (above) and Mather (below) for clones of *Potentilla Drummondii* and *P. Breweri*.

The graphs are constructed from data averaged from 10 individuals of *P. Drummondii Bruceae* and 6 of *Drummondii typica* (both subalpine), 3 of alpine *Drummondii*, and 5 of *P. Breweri*.

the diversity is therefore such that it includes both physiological and morphological characteristics.

CYTOLOGY

The cytological situation in cenospecies *Potentilla Drummondii* is very similar to that in the *P. gracilis* complex, except that no plants

with regular meiosis have been found, and the chromosome numbers are generally higher. There is the same high number of univalents, resulting in very irregular sizes of pollen, or, in extreme cases, in par-

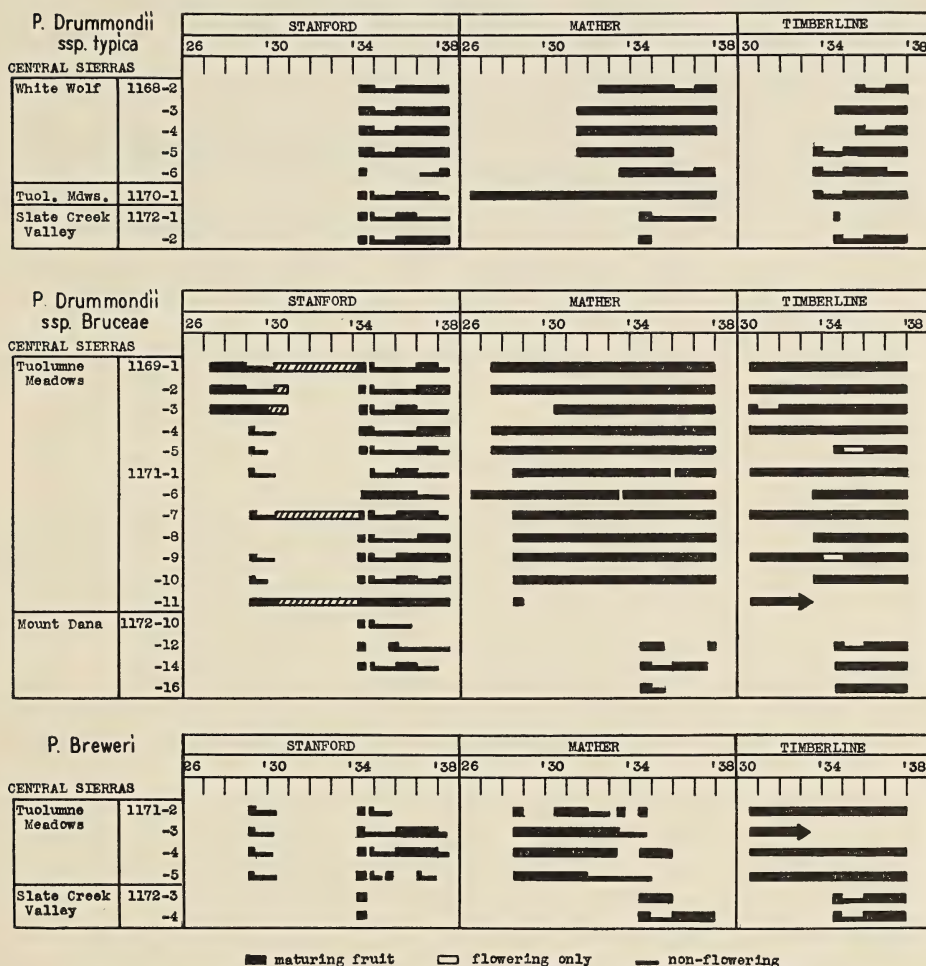


FIG. 76. Record of survival and flowering of clones of *Potentilla Drummondii* and *P. Breweri* at Stanford, Mather, and Timberline.

See table 18 for further data on the individual plants represented. Shaded line indicates that the plant was kept in the lathhouse at Stanford. The scale indicates years.

tial disintegration. Here, also, the chromosome number varies within the population. The chromosomes are similar to those of *gracilis*, although possibly still smaller, and there are similar technical difficulties in counting them.

The following tabulation enumerates the chromosome counts, some of which were made by Miss Ravage:

Potentilla Drummondii typica:

Subalpine ecotype (from White Wolf and Tuolumne Meadows):

1168-2: $2n = ca. 104$ (roots).

1168-4: $2n = ca. 106-108$ (roots).

1168-5: $2n = ca. 105$ (roots).

1168-6: $2n = ca. 96$ in meiosis; 15 to 36 univalents in first metaphase, the others bivalents; some pollen mother cells disintegrate during prophase.

1170-2: $2n = ca. 100$ (mitotic in floral region); $ca. 98-104$ in the first meiotic metaphase; $ca. 12$ univalents; pollen mother cells shriveled; pollen size very irregular, many grains empty.

Alpine ecotype (from Slate Creek Valley):

1172-2: $2n = ca. 92$ (mitotic in floral region); 17 to 30 univalents in first metaphase.

Potentilla Drummondii Bruceae:

Subalpine ecotype (from Tuolumne Meadows):

1169-1: $2n = ca. 64$ (mitotic in floral region).

1169-3: $2n = ca. 69$ (mitotic in floral region), $ca. 71$ (meiotic in first metaphase); 25 to 31 univalents; $30 + 37 + 2$ detached chromosomes seen in second metaphase; pollen mother cells divide into three, four, five, or six cells of different size, some of them with extra-nucleate chromosomes.

1171-1: $2n = ca. 98 + 4$ fragments (mitotic in floral region).

1171-7: $2n = ca. 69$ (roots), $ca. 62-73$ in meiosis; 13 to 28 univalents in diaphase and first metaphase; pollen grains exceedingly variable in size and many dwarfed.

1171-11: $2n = ca. 71$ (roots), $ca. 70$ (mitotic in floral region), $ca. 69$ (meiotic, first metaphase); $ca. 26$ to 35 univalents; $35 + 35$ and $30 + 40$ chromosomes counted in two second metaphases; pollen grains very irregular in size, many empty.

Alpine ecotype (from Mount Dana):

1172-12: $2n = ca. 87$ (somatic in floral region).

1172-14: $2n = ca. 79$ (somatic in floral region); pollen mother cells and nuclei disintegrate.

Potentilla Breweri (from Tuolumne Meadows and Slate Creek Valley):

1171-2: $2n = ca. 102$ (roots), $ca. 99$ (meiotic, first metaphase); 13 to 25 univalents, some of which split in anaphase; second metaphase fairly regular; pollen tetrads fairly regular, very little variation in pollen size, and no dwarf pollen observed; the comparatively large number of bivalents insures fairly regular distribution of chromosomes; possibly sexual.

1171-5: $2n = ca. 72-73$ (mitotic in floral region); up to 23 univalents in first metaphase; pollen of fairly regular size but rather scarce.

1172-3: $2n = ca. 100$ (mitotic in floral region); pollen considerably variable.

In cenospecies *Potentilla gracilis*, it will be recalled, the more robust plants had the highest number of chromosomes and tended to occur at the lowest elevations. No such correlation appears to exist in cenospecies *Potentilla Drummondii*. Plants that differ considerably in chromosome number show very little difference in size. Sub-alpine *P. Drummondii Bruceae* is the form that generally has the lowest chromosome number in this group.

V

STUDIES IN THE GENUS HORKELIA

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Another member of the tribe Potentilleae of the rose family employed in the transplant investigations is *Horkelia*, a genus endemic to western America that has frequently been included in *Potentilla*. *Horkelia* and its close relative *Ivesia* have been revised by Keck (1939). Distribution maps, citation of specimens, and synonymy are given in that publication, so that such details need not be repeated here. Only relatively few forms have yielded sufficient information to warrant their inclusion in this account.

Horkelia roughly parallels the two cenospecies *Potentilla arguta* and *P. gracilis* in its distribution, except that it attains its greatest diversity and development in California and does not truly enter the Rocky Mountain flora. The genus covers almost all the climatic belts from the seacoast to tree line and occurs as high as 3300 m., but differs from *Potentilla glandulosa* in that several *Horkelia* species are needed to cover these belts. The species mentioned in the following pages represent some of this diversity, but are, after all, only a very small sample of the seventeen species and many subspecies of the genus. Almost all the data presented in this chapter deal with one widespread montane species, *Horkelia fusca* Lindl., and two species that are restricted to the California coastal region, *H. californica* C. & S. and *H. cuneata* Lindl.

CYTOLOGY. The chromosome situation in this genus is scarcely more complicated than that in the section *Drymocallis* of *Potentilla*. The chromosome number was $n=7$ for all species examined in that group, but is different in a most interesting way in *Horkelia*. The basic number so far as known is $n=14$ in this genus (Gustafsson, 1940) instead of $n=7$ as in all groups of *Potentilla*. Almost all the species have been shown to be diploid, $n=14$, except two coastal species, *Horkelia californica* C. & S. and *H. marinensis* (Elmer) Crum, both of which are tetraploid, $n=28$. These findings are particularly significant in view of the fact that *Horkelia* has been included in *Potentilla* by many authors.

Dr. Åke Gustafsson, of the Institute of Genetics, University of Lund, Sweden, was a guest in the laboratory of the Carnegie Institution's Division of Plant Biology for some weeks in the summer of 1938 and undertook the cytological examination of *Horkelia* and *Ivesia* at that time. In company with the writers he made field studies and fixations of both genera. He found *Ivesia* species cytologically related to *Horkelia*, and so far as known all are diploid, with $n=14$. His account of the cytology of these two genera is now in press. No crossings have been attempted by us in *Horkelia*.

HORKELIA FUSCA LINDLEY

This species is montane and northern in its distribution. It extends from the Cascades of Washington to the southern Sierra Nevada and east to Yellowstone Park. It is quite variable over much of its range and has six recognized subspecies, but only two of these were included in the transplant experiments. These two were *H. fusca* ssp. *parviflora* (Nutt.) Keck, as it is found in the central Sierra Nevada, and *H. fusca* ssp. *capitata* (Lindl.) Keck, from north-eastern Oregon. In the Sierra Nevada ssp. *parviflora* occupies about the same range of habitats and the same zones as *Potentilla gracilis* ssp. *Nuttallii*. It is found in meadows and on gravelly slopes at altitudes from 1370 to 3300 m. (4500 to 10,800 ft.). In this region the species is not so variable as it is farther north, and only one subspecies is found. Local populations are quite homogeneous. However, the alpine forms react differently from those of mid-altitudes in the transplant experiments, making it evident that they belong to another ecotype. These ecotypes, then, are distinguishable on the basis of physiological reactions and quantitative morphological differences that cannot be used successfully to separate them into subspecies. The relatively small number of clones and localities represented in the experiments has made it impossible to determine whether or not a subalpine ecotype exists in addition to the mid-altitude and alpine ecotypes.

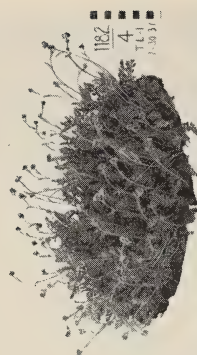
MODIFICATIONS INDUCED BY CLIMATE. Reactions of a clone of the alpine ecotype of *H. fusca parviflora*, when exposed to the radically different climates at Stanford, Mather, and Timberline, are shown in figure 77. This clone came from Slate Creek Valley, near Timberline station. Members of the alpine ecotype are larger at Mather



AT STANFORD



AT MATHER



AT TIMBERLINE

FIG. 77. Modifications in a clone of *Horkelia fusca* at three altitudes.

This plant, 1182-4, was dug August 2, 1927, near Timberline station, at 3050 m., and planted at Mather in 1928; the propagules at Stanford and Timberline were taken from it and set in 1934 and 1930, respectively. The photographs, shown to the same scale, were all taken in 1937.

than in the garden at Timberline, in their native climate. The height is greater, as shown by the graph of averages in figure 79, and the number of flowering stems is appreciably increased, as shown in table 19. From figure 77 the reader gains the impression that the propagule at Stanford is also moderately larger than the one at Timberline, but this is not strictly representative, for the plants ordinarily do not thrive as well at Stanford as at Timberline and their survival is poor (see fig. 82).

The reactions of the mid-altitude ecotype are comparable, except that this form is taller at all stations. This is illustrated in figure 78, which affords an opportunity to compare the modifications of the two Sierran ecotypes at the three stations. One observes their parallel reactions in the three climatic gardens. In each example clone members at Mather are the most thrifty, while those at Timberline are smaller. Those at Stanford are usually still smaller, as is shown by the average heights plotted in the curves in figure 79. Altitudinal differences produce much the same effects on individual characters of *Horkelia fusca* as in *Potentilla* species. Clone members in alpine conditions, as compared with those at mid-altitude, have fewer and shorter flowering stems, smaller basal leaves, with more crowded and thickened leaflets, and somewhat lighter green herbage.

An observation of particular interest made on transplants of both the alpine and mid-altitude ecotypes of *H. fusca parviflora* growing at Berkeley and Stanford is that they do not have a true period of dormancy at these stations, but remain evergreen. Many observations indicate that these forms are definitely dormant in midwinter at Timberline, with old leaves destroyed. Here, then, is a plant that is dormant in winter in its native habitat, but has the capacity to remain evergreen at a lowland station. This behavior is unlike that of any investigated species of *Potentilla*. It may be accounted for by the exceptional hardiness of this species; it is very frost-resistant at Timberline in the late summer and fall and starts to develop new rosette leaves even before the winter snows have completely melted in spring. *Potentillas*, in contrast, do not develop their new leaves before the snow cover of winter has melted away.

Further modifications are shown in table 19. Here, length and number of stems and date of first flowers are tabulated for several clones of each ecotype at the three stations. The most notable modifications shown in this table are between clone members of the mid-



FIG. 78. Modifications in clones of *Horkelia fusca* at three altitudes.

Below: 1181-3, a plant of the mid-altitude ecotype dug July 10, 1927, at Aspen Valley, Yosemite Park, at 1910 m. and planted at Mather in 1928; the propagules at Stanford and Timberline were taken from it and planted in 1934. Above: 1182-5, a plant of the alpine ecotype dug August 2, 1927, near Timberline station, at 3050 m., and planted at Mather in 1928; the propagules at Stanford and Timberline were taken from it and planted in 1934 and 1933, respectively. The specimens were all taken in 1937.

altitude ecotype at each of the stations in regard to number of flowering stems; these differences are very striking and obviously significant. Both ecotypes are markedly most floriferous at Mather. The samples of the mid-altitude and alpine ecotypes differ significantly in

TABLE 19
MODIFICATION IN ECOTYPES OF HORKELIA FUSCA
(Averages from one to three years, 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
MID-ALTITUDE ECOTYPE:									
1180-1, Mather, 1400 m.....	46.7	21.5	208.3	21.5	May 21.5	Aug. 19
-2, Same.....	25	48.7	23.5	3	166.7	7.7	Apr. 25	May 22.5	Aug. 24.0
1181-1, Aspen Valley, 1910 m.....	57.0	22.3	50.0	8.3	May 24.0	Aug. 26.0
-2, Same.....	26	63.0	35	3	100.0	1	May 7	May 28.0	(Aug. 3)
-3, Same.....	29.0	58.3	40.0	3.0	166.7	50.7	May 6.0	May 23.5	Aug. 18.3
-4, Same.....	25	64.3	35.0	3	341.7	9.0	Apr. 28	May 23.5	Aug. 16.0
Means.....	26.3	56.3	29.6	3.0	172.2	16.4	May 2.0	May 23.8	Aug. 20.7
ALPINE ECOTYPE:									
1182-1, Slate Creek Valley, 3050 m.....	(20)	37.0	65.0	(Apr. 15)	May 19.0	Aug. 9.3
-2, Same.....	37.0	6	May 19.0
-3, Same.....	15.0	38.0	20.7	1.0	81.7	11.3	Apr. 22	May 17.5	Aug. 4.3
-4, Same.....	21	39.0	22.3	90	141.7	108.3	Apr. 5	May 17.5	Jul. 30.3
-5, Same.....	19.5	30.7	18.3	16.0	25.0	7.0	Apr. 15.0	May 19.0	Aug. 2.8
Means.....	18.5	36.3	20.4	35.7	63.9	42.2	Apr. 14.0	May 18.4	Aug. 3.7

Difference of stem length, mid-altitude minus alpine ecotypes at Mather: 20.0 cm. \pm 3.32; t = 6.02 (highly significant).

stem length at Mather, as may be seen at the bottom of the table. The graph, figure 79, shows that *Horkelia fusca capitata*, which is a montane ecotype from Oregon and normally larger than any of the forms of ssp. *parviflora*, maintains its relative tallness at both Stanford and Mather.

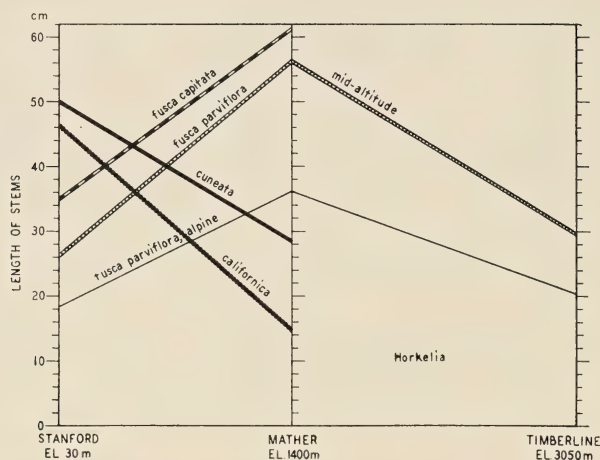


FIG. 79. Modifications in length of stems at three altitudes in clones representing various ecotypes and ecospecies of *Horkelia*.

Graphs constructed from data averaged from the years 1935 to 1937 for the plants listed in tables 19 and 21. *Horkelia cuneata* and *californica* do not survive at Timberline.

DIFFERENCES IN EARLINESS. The mean dates on which first flowers appear at the three transplant stations are tabulated in table 19 and graphed in figure 80. At all three stations the alpine ecotype of *H. fusca parviflora* is consistently earlier than the mid-altitude ecotype, although this difference is least apparent at Mather; at Timberline and Stanford, the mid-altitude and alpine ecotypes flower, on an average, more than two weeks apart.

Different ecotypes of one species may have very dissimilar capacities for responding to the same influences in the environment. This point is demonstrated by a comparison of the annual fluctuations in earliness between the mid-altitude and alpine ecotypes of *H. fusca parviflora*. These are presented as graphs in figure 81. For these plants 1934 was an early year at both Mather and Timberline. As previously shown for the ecotypes of *Potentilla glandulosa* and *P. gracilis*, and as substantiated by the reactions of *Horkelia*, 1936 was an early year at Mather but a late year at Timberline. The mid-

altitude ecotype of *Horkelia fusca* was considerably more responsive to these influences than was the alpine ecotype, which was not hastened unduly at Mather in 1936 nor appreciably delayed at Timber-

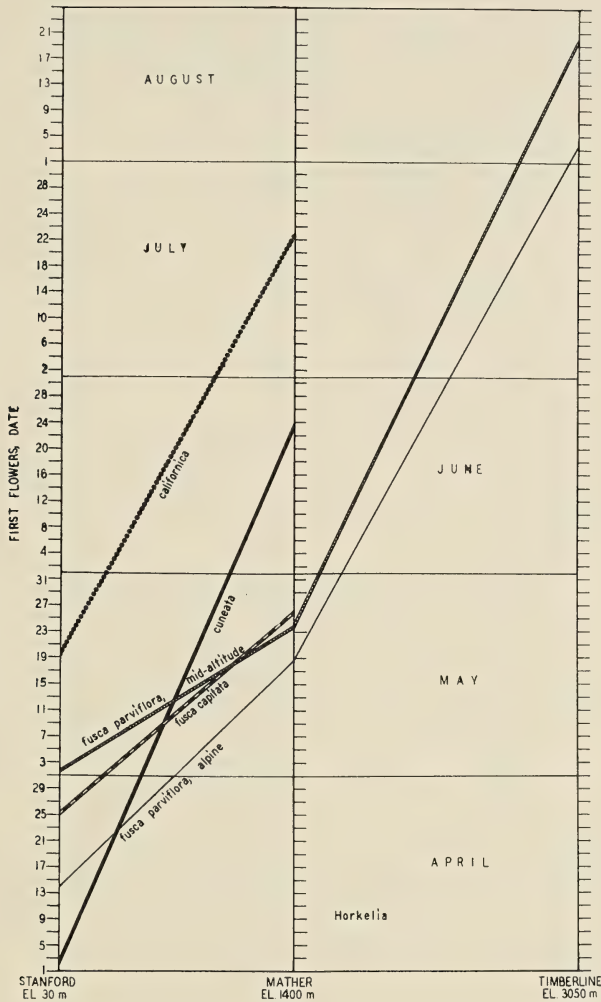


FIG. 80. Modifications in date of first flowers at three altitudes in clones representing various ecotypes and ecospecies of *Horkelia*. Data from the same sources as in figure 79.

line in the same year. In this respect, the alpine ecotype compares with *Potentilla diversifolia* and the entire cenospecies of *P. Drummondii*.

In the preceding chapters on *Potentilla* it has been mentioned

that, in general, plants of that genus which are not able to reach flower by approximately the tenth of August at Timberline cannot mature their seed before heavy frosts terminate their growth. Using that estimate with *Horkelia*, we find that even in the late year 1936 the alpine ecotype of *fusca* could be expected to

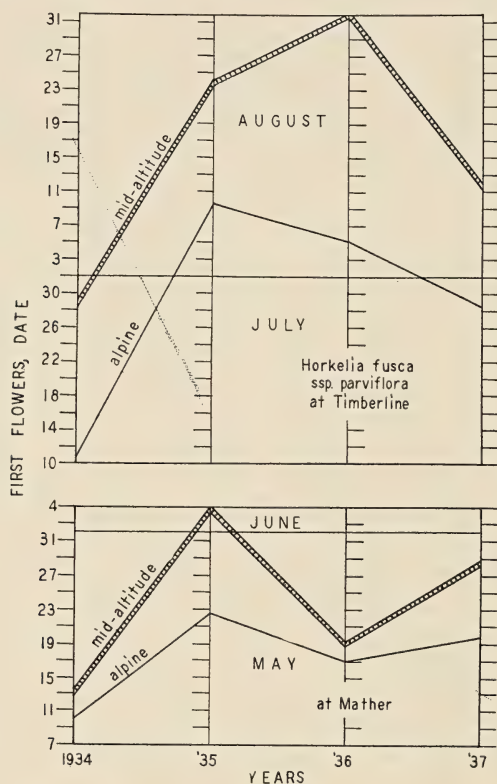


FIG. 81. Yearly variations in dates of first flowers at Timberline (above) and at Mather (below) in clones representing mid-altitude and alpine races of *Horkelia fusca* ssp. *parviflora*.

Graphs constructed from data averaged for the plants listed in table 19.

ripen fruit, whereas in two years, and possibly three, out of the four-year period graphed, the mid-altitude ecotype could not. Actual observation proved this expectation. Within the period from 1934 to 1937 it was found that on the basis of twenty-four annual observations on six individuals, the mid-altitude ecotype was able to flower 83.4 per cent of the years, but was able to ripen fruit only 8.3 per cent of the years. At the same time seventeen annual observations on

four individuals of the alpine ecotype showed flowering every year and ripening of fruit in all but one, or an average of 94.1 per cent. These differences are shown graphically in the survival chart (fig. 82).

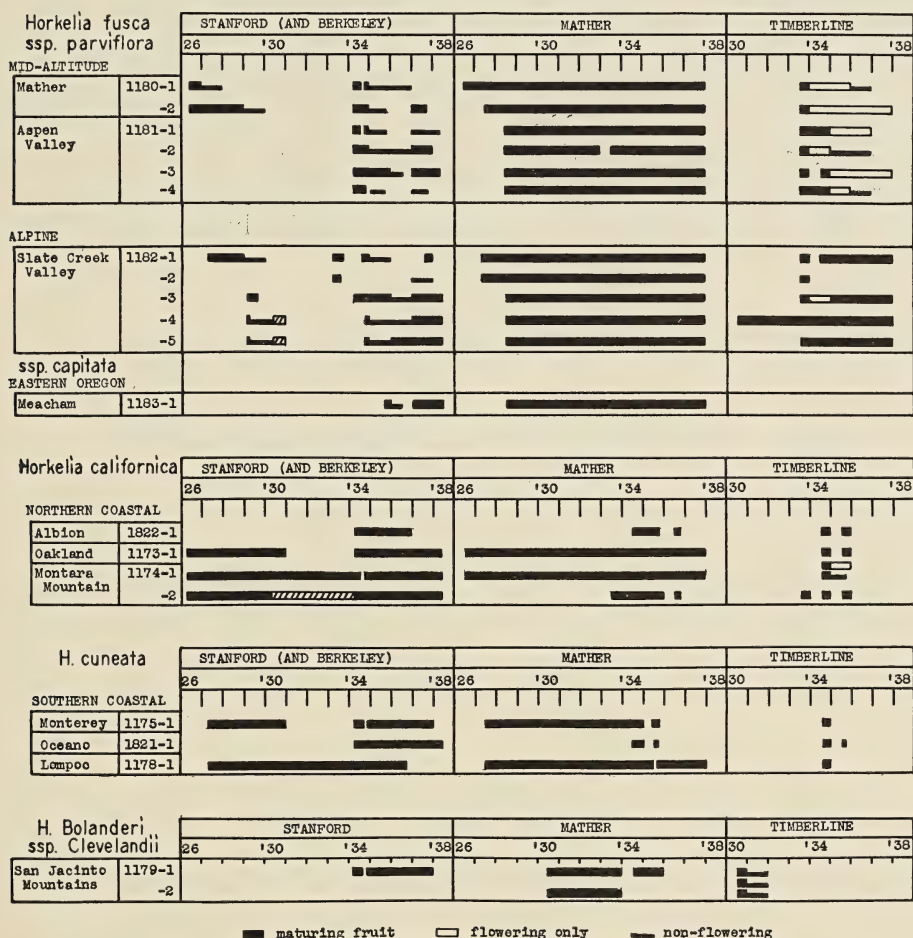


FIG. 82. Record of survival and flowering of clones of various *Horkelia* species at three altitudes.

See tables 19 and 20 for more detailed data concerning most of the individuals represented above. The scale indicates years. Shaded line indicates that the individual was kept in a lathhouse at Stanford.

Another factor must be considered in connection with earliness in the ecotypes of *H. fusca*. It takes longer for these *Horkelias* to ripen their seed than for the *Potentillas*. This disadvantage, however, is more than compensated for by their marked frost resistance, which

enables them to carry on their normal functions at Timberline for a longer period. This throws the balance in favor of the *Horkelias*, when they are compared with less hardy species that blossom at the same time.

EFFECT OF LOCAL ENVIRONMENTAL DIFFERENCES AT TIMBERLINE. Mention has previously been made of the slope garden at the alpine station, which is not far removed from the interstation garden but is in a more sheltered position. Results of interest have come from three plants of *Horkelia fusca* in that plot. They are shown in table 20. Members of the two ecotypes are statistically almost indistin-

TABLE 20
COMPARISON OF ECOTYPES OF *HORKELIA FUSCA* IN THREE SIERRAN GARDENS, BASED LARGELY UPON THREE-YEAR AVERAGES

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			DATE OF FIRST FLOWERS		
	Mather	Timberline		Mather	Timberline	
		Meadow	Slope		Meadow	Slope
MID-ALTITUDE ECOTYPE:						
1180-2, Mather, 1400 m.	48.7	23.5	43.0	May 22	Aug. 24	Aug. 22
1181-1, Aspen Valley, 1910 m. . .	57.0	22.0	44.0	May 24	Aug. 26	Aug. 24
Means.	52.9	22.9	43.5	May 23	Aug. 25	Aug. 23
ALPINE ECOTYPE:						
1182-1, Slate Creek, 3050 m.	37.0	43.0	May 20	Aug. 9
-3, -4, -5, Same.	35.9	20.4	May 18	Aug. 2
Means.	36.5	20.4	43.0	May 19	Aug. 2	Aug. 9

guishable as to height both in the meadow (interstation garden) and on the slope. The modification in height that these plants show on being moved from the meadow to the slope is far more spectacular than the heritable differences between the two ecotypes. In fact, the clone members of the mid-altitude ecotype on the Timberline slope become almost as tall as those at Mather, at 1650 m. less altitude, and the single slope-grown plant of the alpine ecotype even surpassed its clone member at Mather, according to three-year averages. Under all three conditions the alpine ecotype is significantly

earlier than the other, so that although the two become alike morphologically at Timberline, the difference in earliness becomes accentuated there!

In conclusion it should be mentioned that while morphologically the mid-altitude and alpine ecotypes of *Horkelia fusca* do not differ as profoundly as similar ecotypes in *Potentilla glandulosa* and *P. gracilis*, physiologically they appear to be as different as these.

SURVIVAL AND DEGREE OF FLOWERING. Both the mid-altitude and alpine ecotypes of *Horkelia fusca* survive and flower equally well at Timberline, as may be seen in figure 82, although only the alpine ecotype can produce ripe seed every year. At Mather both thrive, ripen fruit, and survive. At Stanford they are not vigorous or long-lived, but have a marked tendency to remain in a non-flowering state. Oddly enough, clone members of the mid-altitude ecotype are weaker and less floriferous here than some members of the alpine ecotype.

The mid-altitude ecotype of *Horkelia fusca* reacts at Stanford in a manner usual for plants from subalpine and alpine altitudes; its stems are shorter than at Timberline, it has less vigor and poor survival, and it tends to remain in the vegetative stage for several years. It is therefore possible that the forms of *Horkelia fusca* from middle altitudes actually represent a subalpine ecotype that is pioneering at lower elevations. This gains credence from the fact that while this plant is common at higher elevations, it is very rare at its lower limit at Mather.

COAST RANGE SPECIES

Two species from the Outer Coast Range of California which have been used in the transplant experiments will be discussed collectively, since their reactions to different environments show so many features in common. These are *Horkelia californica* Cham. & Schlecht., a plant common on grassy slopes overlooking the ocean from Humboldt Bay to Santa Cruz County, and *H. cuneata* Lindl., frequent along the coast from San Francisco Bay to southern California. Both are evergreen perennial herbs like the *Potentillas* of the preceding chapters, but neither has produced an ecotype adapted to the interior valleys or mountains of California.

A clone of *H. californica* is depicted as it appears at the three transplant stations in figure 83. The chief interest that has devel-



FIG. 83. Modifications in a clone of *Horkelia californica* at three altitudes.

This plant, 1174-1, was dug February 9, 1926, at Montara Mountain, San Mateo County, California, at 215 m., grown at Berkeley until 1929, then moved to Stanford; propagules from it were set at Mather in 1926 and at Timberline in 1934. The specimens were taken at Stanford and Timberline in 1935 and at Mather in 1934.

oped from the experiments on this and the other coastal species is in their seasonal reactions at different altitudes. Like many species of the Coast Ranges, these *Horkelias* are evergreen in their native habitats and in the gardens at Berkeley and Stanford. Their most active vegetative growth takes place toward the end of the rainy season in the spring months, but it starts as early as the first rains of November. In spite of occasional frosts through the winter, they develop new rosette leaves almost continuously. Precocious flowers may develop in mild winters, but the principal flowering occurs in spring. These plants utilize the long growing season at the lowland stations to the full and become rather massive, but very little growth takes place during the dry late summer and fall.

At Mather, on the other hand, these species are forced to change their customary seasonal habits because of the relatively severe winters. Growth is restricted to the summer period between May and September. With the beginning of spring growth, new basal leaves and flowering stems develop from buds at ground level in the crown. Late frosts frequently injure the new foliage, and repeated freezing often weakens the plants considerably.

In these species the Mather propagule never attains a bulk comparable with that of the one at Stanford, for the stems are both shorter and fewer. This is shown in table 21 and figure 79. This reduction is far greater than the slight decrease in the Coast Range ecotype of *Potentilla glandulosa*, for in *Horkelia* the Mather clone members are reduced to between one-half and one-third the size of those at Stanford. Also, the reduction in number of stems is far greater in these *Horkelias* than in *Potentilla glandulosa*, in which it is almost imperceptible. This correlates with the fact that the two *Horkelias* are strictly coastal, whereas *Potentilla glandulosa typica* is a Coast Range ecotype that ascends to a rather high elevation.

The two coastal *Horkelias* tend to be less glandular-viscid at Mather, a development that seems to be associated with age, for vegetative growth does not reach the degree of maturity possible at the coastal stations.

Flowering is much delayed at Mather, as is shown in table 21 and figure 80. This delay appears to be characteristic for coastal ecotypes and ecospecies, for, as will be seen later, the performance is repeated in *Zauschneria*, *Achillea*, and *Artemisia*. There is also a resemblance between the reaction of these *Horkelias* and that of *Potentilla glandu-*

losa typica, which is relatively delayed at Mather. However, the delay in the coastal *Horkelias* is greater, for *cuneata* blooms one month and *californica* two months later than *P. glandulosa typica*. This late average at Mather has been compiled from many observa-

TABLE 21
MODIFICATIONS IN *HORKELIA CALIFORNICA* AND *HORKELIA CUNEATA*
(Averages from three years at Stanford, one to three years at Mather)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)		NUMBER OF STEMS		DATE OF FIRST FLOWERS	
	Stanford	Mather	Stanford	Mather	Stanford	Mather
<i>Horkelia californica</i> :						
1822-1, Albion, Mendocino Co., 90 m.	50.0	13	62.5	6	(Jun. 20)	Aug. 5
1173-1, Oakland Hills, 215 m.	38.0	15	30.3	2	May 24	Jul. 12
1174-1, Montara Mt., 215 m.	40.0	22.3	40.0	19.3	May 18	Jul. 19
-2, Same.	44.7	20.5	31.7	19.0	May 15	Aug. 5
Means.	43.2	17.7	41.1	11.6	May 19.0	Jul. 25.8
<i>Horkelia cuneata</i> :						
1175-1, Monterey, 100 m.	51.0	15	27.0	1	Apr. 8	Jun. 25
1821-1, San Luis Obispo Co., 10 m.	34.0	28.7	Mar. 30
1178-1, Lompoc, Santa Barbara Co., 120 m.	65.0	42	65.0	17	Apr. 1	Jun. 22
Means.	50.0	28.5	40.2	9.0	Apr. 2.5	Jun. 23

() Not included in means.

tions in the interstation garden and has been supplemented by the flowering behavior of these species in the water-light gardens, in which *californica* blooms in the middle of July, and *cuneata* in the latter half of June.

At Stanford, *H. cuneata* is early flowering, for it is in bloom the first of April, more than six weeks ahead of *H. californica*. The retardation at Mather may be explained on the assumption that the

long pre-flowering vegetative period of these species in their native habitats and in the lowland gardens builds up reserves, and is a necessary forerunner to the reproductive processes.

Both *californica* and *cuneata* are able to produce ripe seed by the end of summer at Mather, but their flowering stems are more poorly developed than those of propagules at Berkeley and Stanford, and development of the rosette is much more restricted.

Winter killing of the coastal species of *Horkelia* is frequent at Mather, an indication that the factors necessary for winter survival in cool-temperate climates are lacking. Thirteen propagules of *H. californica* attained an average age of only thirty-four months, and eleven propagules of *H. cuneata* survived for an average of only twenty months. This is an additional distinction from *Potentilla glandulosa typica*, which survives very well at Mather.

At Timberline, clone members of *H. californica* and *cuneata* seldom survive even a single winter (fig. 82), in this respect resembling the coastal ecotype of *Potentilla glandulosa*. One of these survivors is pictured in figure 83. During the early year 1934 it was able only to pass through the first stages of spring growth and produce a small rosette and immature flowering stems. The Coast Range ecotype of *P. glandulosa* produced ripe seed at Timberline that same year. It is well to emphasize again, in connection with this figure, that the modifications imposed upon the clone by the very different environments did not obliterate the individuality of the plant. The same rule applies to all species of *Horkelia* that have entered the experiments.

Horkelia californica and *cuneata* produce longer flowering stems in shade at Mather than in full sun. Shade-produced stems of *californica* at Mather approach in length those developed in the full sun at Berkeley or Stanford—a fact that might suggest that the more intense light at Mather may be a factor in shortening stems. But stem length is also increased in shade at Berkeley and Stanford, although to a relatively less extent. Shade enlarges leaves and makes stems more prostrate or lax at either altitude.

Horkelia tenuiloba (Torr.) Gray is another, but rare, Coast Range species, distributed chiefly on chaparral-covered slopes north of San Francisco Bay, that has been tested in the transplant experiments. Its reactions were similar to those of *cuneata* and *californica*, except that the plant is more delicate and survives less well.

A small amount of data has been obtained from a species of southern California, *H. Bolanderi* Gray ssp. *Clevelandii* (Greene) Keck. Our material, from the San Jacinto Mountains, Riverside County, has yielded a modicum of information, the most interesting item of which is its survival record at the three stations, as shown in the graph, figure 82. Although it came from an original elevation of more than 1500 m., it survives about the same as the coastal species, to which it has a strong habital resemblance.

VI

THE GENUS ZAUSCHNERIA

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The power of experimental methods in elucidating plant relationships has been most clearly demonstrated in *Zauschneria*. The innumerable intergradations of form within this genus have long puzzled botanists who depended on morphological criteria alone. Now, however, the relationships have become so clarified that one can evaluate with assurance the systematic rank of the various forms. A brief discussion of the main subdivisions of the genus, based upon all the available facts, will be presented first in order to aid in understanding the results of the varied-environment experiments. Following the discussion of these experiments, a review of the cytogenetical studies will be given, which, in the light of the other evidence, brings into clear relief different degrees of relationship between the forms.

PRINCIPAL SUBDIVISIONS

Zauschneria is composed of two groups as to chromosome number, one with 15 pairs (diploid), and the other with 30 (tetraploid). Four species in all are recognized. Three of these are monotypic, but the fourth is composed of three morphologically distinguishable ecotypes or subspecies. Figure 84 shows typical representatives of these six groups. Living plants of all but *Z. Garrettii* are shown in figure 85.

The three monotypic species compose the diploid group. These are: (1) *Zauschneria cana* of the coastal regions of southern and central California, (2) *Z. septentrionalis* of northern California, and (3) *Z. Garrettii* of the Wasatch and Rocky Mountains. *Zauschneria cana* is a suffrutescent, bushy plant with narrowly linear, canescent leaves. It occurs in a narrow zone along the coast for a distance of about three hundred miles (500 km.). *Zauschneria septentrionalis* is herbaceous and low, almost matlike, and has oval or elliptic leaves that vary from silvery-canescant to almost green. It occupies an

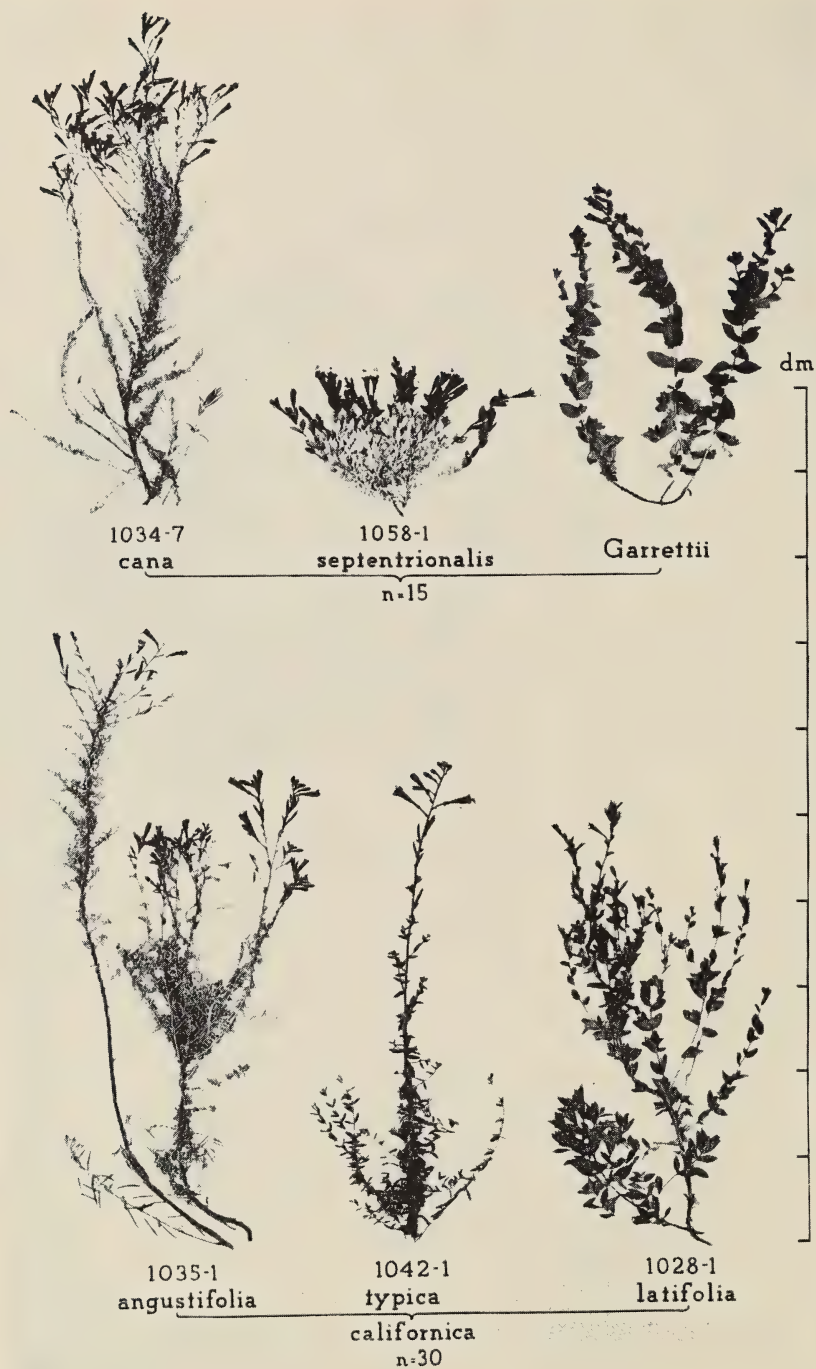


FIG. 84
(Legend on opposite page)

area in the center of the Coast Redwood region about sixty-five miles (100 km.) in length, mainly along the Eel, Mattole, and part of the Trinity river basins. *Zauschneria Garrettii* is taller and larger-leaved than *septrionalis*, but resembles it in being herbaceous. The isolated distribution of this species in Utah and western Wyoming separates it geographically from the other *Zauschnerias*.

The tetraploid group is considered to be a single species, *Z. californica*, with three ecotypes or subspecies: (1) ssp. *angustifolia*, a narrow-leaved woody plant with much the same distribution as *Z. cana*; (2) ssp. *latifolia*, a herbaceous type with large elliptical leaves that occurs from the Coast Ranges of southwestern Oregon and northern California, where it is found just to the east of *septrionalis*, through the Sierra Nevada to the mountains of southern California, Arizona, and northern Sonora; it is also in the mountains of northeastern Nevada; and (3) ssp. *typica*, which is intermediate in character between *angustifolia* and *latifolia*, and occurs in the California Coast Ranges and southward at low elevations to northern Baja California.

While all six units represent distinguishable ecotypes that occur in quite well-defined geographical ranges, much variation exists within each, making borderline forms very difficult to identify. Especially the tetraploid complex, *Z. californica*, is variable; the characters of subspecies *angustifolia* grade into *typica*, and those of *typica* into *latifolia*. Even the diploid and tetraploid groups are not distinguished from each other by clear-cut characters. For example, *Z. cana* ($n=15$) and *Z. californica* ssp. *angustifolia* ($n=30$) are frequently so much alike that taxonomists have confused them, since the two occupy common territory. Similarly, some forms of *Z. septrionalis* ($n=15$) so closely approach *Z. californica* ssp. *latifolia*

FIG. 84. Representatives of the major taxonomic groups in *Zauschneria*.

Below: the three subspecies of tetraploid *Z. californica*: 1035-1 (*angustifolia*) from near Avalon, Catalina Island, at 30 m.; 1042-1 (*typica*) from near the summit of Parkfield Grade, Monterey County, at 1100 m.; 1028-1 (*latifolia*) from Fern Valley, San Jacinto Mountains, Riverside County, at 1370 m.

Above: the three diploid species: 1034-7 (*Z. cana*) from near Palos Verdes, Los Angeles County, at 60 m.; 1058-1 (*Z. septrionalis*) from Bolling Grove, Humboldt County, at 300 m.; and *Z. Garrettii*, from Big Cottonwood Canyon, Salt Lake County, Utah, at 1675 m. All but *Z. Garrettii* are from California.

The specimens were taken from transplants grown at Stanford, except *Garrettii*, which is a field collection by Milo S. Baker, no. 8552.

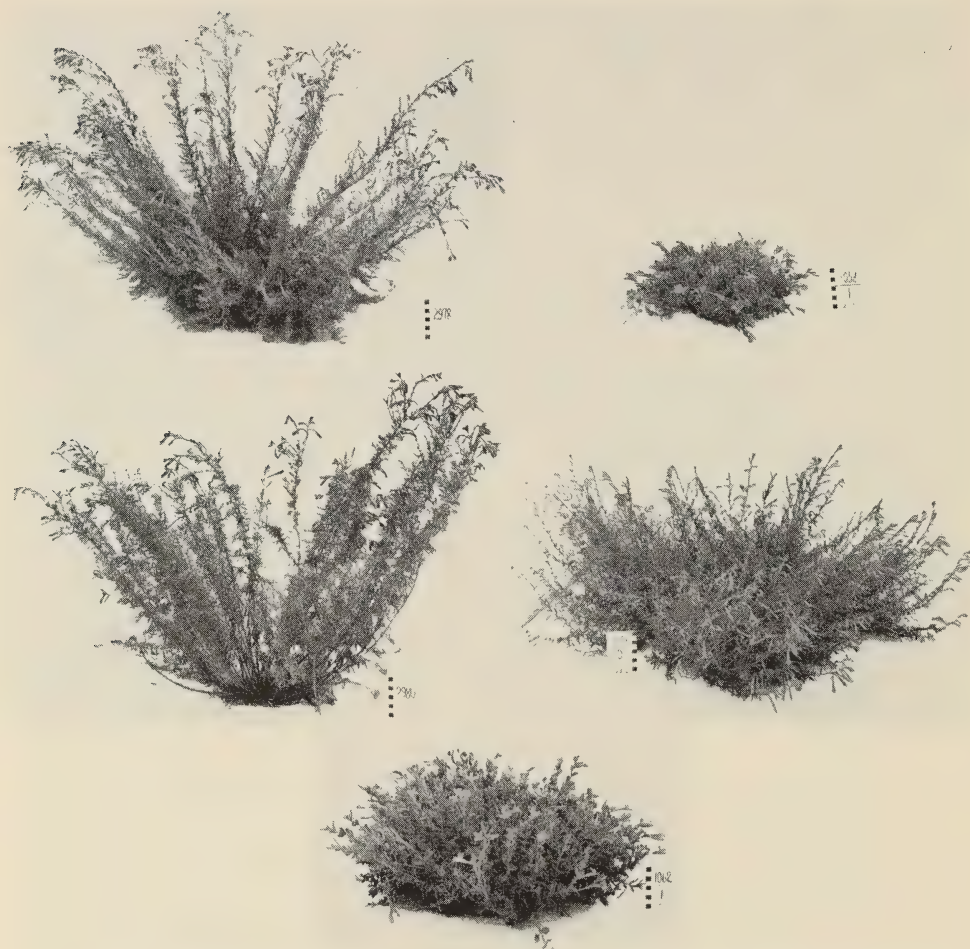


FIG. 85. Living representatives of major taxonomic groups of *Zauschneria* from California.

Top row: two diploid species: 2978 (*Z. cana*), a seedling of 1034-7 from Palos Verdes, Los Angeles County, at 60 m.; 1058-1 (*Z. septentrionalis*), a transplant from Bolling Grove, Humboldt County, at 300 m.

Center row and bottom: three subspecies of tetraploid *Z. californica*: 2980 (ssp. *angustifolia*), a seedling of 1035-1 from near Avalon, Catalina Island, at 30 m.; 1044-5 (ssp. *typica*), a transplant from near Jamesburg, Monterey County, at 1220 m.; and 1062-1 (ssp. *latifolia*), a transplant from near Del Loma, Trinity County, at 375 m.

All photographs taken in 1937, shown to the same scale; plant 1044-5 is at Mather, the others at Stanford.

($n=30$) that they may easily be misidentified. In this case, also, the two groups meet in common territory. *Zauschneria Garretti* ($n=15$) resembles *californica* ssp. *latifolia* sufficiently so that at one

time it was thought possible the two might be of the same species. But they have characteristic morphological differences by which they may be recognized, in addition to the dependable distinctions of chromosome number and geographical separation.

An example of the occasional geographic proximity of some of these units is their distribution on Mount Wilson, in southern California. Around the summit, from 1800 down to 1500 m. elevation, the tetraploid *Z. californica* ssp. *latifolia* occurs exclusively. It is replaced by ssp. *typica* at about 1000 m., while from 670 m. downward this, in turn, is replaced by the diploid *Z. cana*.

TAXONOMY

The systematic units within *Zauschneria* are defined with greater precision in the following taxonomic summary. In this treatment synonymy is given in less detail than in the taxonomic accounts of *Potentilla*, but for the benefit of those who are interested in the disposal of earlier proposals, all published names are listed under their respective present-day units. Types of almost all of these have been seen. The distribution of the California *Zauschnerias* is mapped in figure 86.

KEY TO THE SPECIES AND SUBSPECIES OF ZAUSCHNERIA

- A. Herbaceous throughout; leaves broadly lanceolate to oval, the principal ones more than 6 mm. wide.
 - B. Broadest leaves 5 to 8 (rarely 10) mm. wide, subentire, the lower leaves usually white-canescenscent, rarely green and merely pilose; stems less than 20 cm. long, matted; $n = 15$. Coast Redwood region of Humboldt and northern Mendocino counties, California.....1. *Z. septentrionalis*
 - BB. Broadest leaves 7 to 15 mm. wide, not white-canescenscent.
 - C. Leaves rather coriaceous, the lateral veins evident, \pm sharply denticulate, green, glabrate to pilose but never tomentose, obscurely if at all glandular, broadly ovate, never lanceolate; $n = 15$. Utah and Wyoming.....2. *Z. Garrettii*
 - CC. Leaves not coriaceous, the lateral veins obscure, subentire to denticulate, glabrate to tomentose, variously pubescent, often glandular, broadly lanceolate to oval or ovate; $n = 30$. Montane;



FIG. 86. Distribution of the California forms of *Zauschneria*, as determined from available collections, including those in fourteen herbaria.

southwestern Oregon to the Trinity Alps; Sierra Nevada to southwestern New Mexico and northern Mexico; northern Nevada. . . 3b. *Z. californica* ssp. *latifolia*

AA. Suffrutescent at base; leaves linear to lanceolate, usually less than 6 mm. wide.

D. Stems slightly woody; leaves linear-lanceolate to broadly lanceolate, usually 3 to 5 (rarely to 7) mm. wide, green- to gray-pilose, not canescent; $n = 30$. Principally in the Coast Ranges of California, southward to Baja California. 3a. *Z. californica* ssp. *typica*

DD. Stems obviously woody at base; leaves filiform to narrowly linear, up to 3.5 mm. wide, densely tomentose-canescant. Coastal southern California.

E. Leaves linear, 2.5 to 3.5 mm. wide, moderately fasciculate; flowers 30 to 40 mm. long; $n = 30$. Monterey County to San Diego County. 3c. *Z. californica* ssp. *angustifolia*

EE. Leaves filiform or nearly so, not over 2 mm. wide, very densely fasciculate; flowers 25 to 35 mm. long; $n = 15$. Monterey County to Los Angeles County; possibly in San Diego County. 4. *Z. cana*

1. *Zauschneria septentrionalis* Keck sp. nov.

Herba perennis caespitosa 8–20 cm. alta; foliis aggregatis haud fasciculatis lanceolato-ellipticis vel ovalibus vix acutis 10–25 mm. longis 4–8 rare 10 mm. latis subintegris vel remote et obscure denticulatis concoloribus utrinque dense canescentibus, superioribus plerisque viridibus glandulari-pubescentibus, interdum foliis omnibus viridibus moderate villosis; floribus plerisque 28–32 mm. longis.

Type: *Joseph P. Tracy 5942*, taken August 21, 1921, on barren rock ledges at the mouth of the South Fork of the Trinity River, Humboldt County, California, at 150 m. elevation (Herbarium of the University of California, no. 249614).

Principally confined to the valleys of the Mattole, Eel, and the South Fork of the Trinity rivers, from Hoopa Valley, Humboldt County, to Laytonville, Mendocino County, and southwestern Trinity County, California, at elevations from 50 to 300 m.

2. ZAUSCHNERIA GARRETTII A. Nels., Proc. Biol. Soc. Wash. 20:36, 1907

Zauschneria latifolia var. *Garrettii* Hilend, Amer. Jour. Bot. 16:66, 1929.

Distributed in the mountains from western Park County to Lin-

coln County, western Wyoming, and through the Wasatch Range of Utah to Zion National Park and near Kanab. Apparently the same species grows also in the Abajo Mountains, San Juan County, Utah.

3. *ZAUSCHNERIA CALIFORNICA* Presl, Rel. Haenk. 2:28, t. 52, 1831

3a. *Zauschneria californica* ssp. *typica* Keck nom. nov.

Zauschneria californica Presl, loc. cit.

Zauschneria californica var. *typica* Hilend, Amer. Jour. Bot. 16:61, 1929.

Zauschneria mexicana Presl, loc. cit.

Zauschneria villosa Greene, Pittonia 1:27, 1887.

Zauschneria Eastwoodae Eastw. & Moxley, Southwest Sci. Bull. 1:23, 1920.

Zauschneria velutina Eastw. ex Moxley, *ibid.* 25.

Zauschneria californica var. *villosa* Jeps., Man. Fl. Pl. Calif. 667, 1925.

Valleys and foothills from Sonoma and Lake counties, California, southward through both the Inner and Outer Coast Ranges to coastal southern California and northern Baja California; rare in the lowest foothills of the Sierra Nevada; found from near sea level up to about 1500 m.

3b. *Zauschneria californica* ssp. *latifolia* (Hook.) Keck comb. nov.

Zauschneria californica var. *latifolia* Hook., Bot. Mag. t. 4493, 1850.

Zauschneria latifolia Greene, Pittonia 1:25, 1887.

Zauschneria tomentella Greene, *ibid.* 26.

Zauschneria arizonica Davidson, Bull. So. Calif. Acad. Sci. 1:5, 1902.

Zauschneria argentea A. Nels., Proc. Biol. Soc. Wash. 18:173, 1905.

Zauschneria glandulosa Moxley, Bull. So. Calif. Acad. Sci. 15:22, 1916.

Zauschneria viscosa Moxley, *ibid.*

Zauschneria crassifolia Rydb., Fl. Rocky Mts. 590, 1064, 1917.

Zauschneria Pringlei Eastw. ex Moxley, Southwest Sci. Bull. 1:26, 1920.

Zauschneria elegans Eastw. ex Moxley, *ibid.*

Zauschneria Hallii Moxley, *ibid.* 27.

Zauschneria pulchella Moxley, *ibid.*

Zauschneria canescens Eastw. ex Moxley, *ibid.* 29.

Zauschneria orbiculata Moxley, Bull. So. Calif. Acad. Sci. 19:30, 1920.

Zauschneria pulchella var. *adpressa* Moxley, *ibid.* 20:54, 1921.

Zauschneria latifolia var. *tomentella* Jeps., Man. Fl. Pl. Calif. 667, 1925.

Zauschneria latifolia var. *viscosa* Jeps., *ibid.*

Zauschneria latifolia var. *typica* Hilend, Amer. Jour. Bot. 16:64, 1929.

Zauschneria latifolia var. *arizonica* Hilend, *ibid.* 67.

Zauschneria latifolia var. *Johnstonii* Hilend, *ibid.*

Rocky hillsides and canyons from the Coast Ranges of south-

western Oregon, where it is found not far above sea level, to Trinity County, California, and along the west flank of the Sierra Nevada from Lassen and Plumas counties southward to the mountains of southern California at elevations of 1000 to 2700 m.; southward to the Sierra San Pedro Martir, Baja California; eastward across Arizona to southwestern New Mexico and northern Sonora, and across the Sierra Nevada to the ranges in northern Nevada.

3c. *Zauschneria californica* ssp. *angustifolia* Keck ssp. nov.

Caulibus erectis ad 70 cm. altis deorsum plus minusve suffrutescentibus; foliis dense canescentibus anguste linearibus vel lineari-lanceolatis 2.5–3.5 mm. latis fasciculatis; floribus 30–40 mm. longis.

Type: *Keck 1905*, taken September 30, 1932, at Dana Point, north of San Juan Capistrano, Orange County, California, at 15 m. elevation (Dudley Herbarium of Stanford University).

At low elevations and approximate to the coast of California from central Monterey County to San Diego County, and on Santa Catalina Island. This area is occupied also by ssp. *typica* and *Z. cana*, but the three forms do not mingle to any appreciable extent.

4. *ZAUSCHNERIA CANA* Greene, Pittonia 1:28, 1887

Zauschneria californica var. *microphylla* Gray ex Brew. & Wats., Bot. Calif. 1:218, 1876.

Zauschneria microphylla Moxley, Southwest Sci. Bull. 1:22, 1920.

Range similar to that of *californica* ssp. *angustifolia*, but found on Santa Cruz Island in addition, and not on Santa Catalina Island. Not common except between Point Conception and Point Vicente; extending inland only in Los Angeles County.

According to the cytogenetic evidence presented below, these four species are ecospecies of one cenospecies. In other words, the genus *Zauschneria*, so far as known, is composed of one cenospecies. Were it desirable to refer to this cenospecies by name, it should be called cenospecies *Zauschneria californica*. By the same criterion and those of the transplant experiments, the subspecies of the tetraploid *Z. californica* are ecotypes.

COMPARISON OF THE FORMS IN THREE ENVIRONMENTS

The first transplants of *Zauschneria* were collected in 1923, and since that time many additions have been acquired. Plants from the

southern boundary of California to Humboldt County and from altitudes ranging between sea level and 2740 m. are now in culture, in addition to a few representatives from Arizona and Utah. This collection represents all the six taxonomic groups and includes approximately 200 individuals. Of these, 104 of the most critical were distributed as clone transplants to Stanford, Mather, and Timberline. *Zauschneria Garrettii* has been poorly represented, so the following discussion will be confined to the results from the other five groups.

SEASONAL DEVELOPMENT. *Zauschnerias* bloom late in the fall and require a long preliminary growing period. Therefore, the great differences in length of the growing seasons at the three transplant stations have a profound influence on their development.

At Stanford spring growth on all forms begins about the middle of February. Development then proceeds slowly and steadily until flowering time, which continues from mid-August to November. Frosts afterward induce a greater or less degree of dormancy, depending on the species or form. All species and ecotypes attain complete seasonal maturity at Berkeley and Stanford, producing ripe seeds in abundance.

At Mather the growing season is so much shorter that it permits only partial development of the more slowly maturing types. The diploid *Zauschneria cana* seldom reaches even the first stages of flowering, and other forms flower but fail to mature seed, but some individuals of *Z. californica* ssp. *latifolia* succeed in ripening seed each year.

At Timberline the growing season is so short that none of the species are able to produce more than juvenile spring shoots before they are again subjected to winter weather. No transplant of this genus has ever been observed to produce even flower buds there.

Figure 87 shows in graphic form the relative lengths of the vegetative and reproductive periods of the ecotypes and ecospecies at the three stations. It also shows the average dates when growth starts and flowering begins. The broken lines at the ends of the Mather and Timberline columns indicate the approximate proportion of plants failing to produce some ripe seed during the four-year period.

The vegetative period at Mather is remarkably shortened. Although growth starts there at least three months later than at Stanford, flowering begins at both stations at approximately the

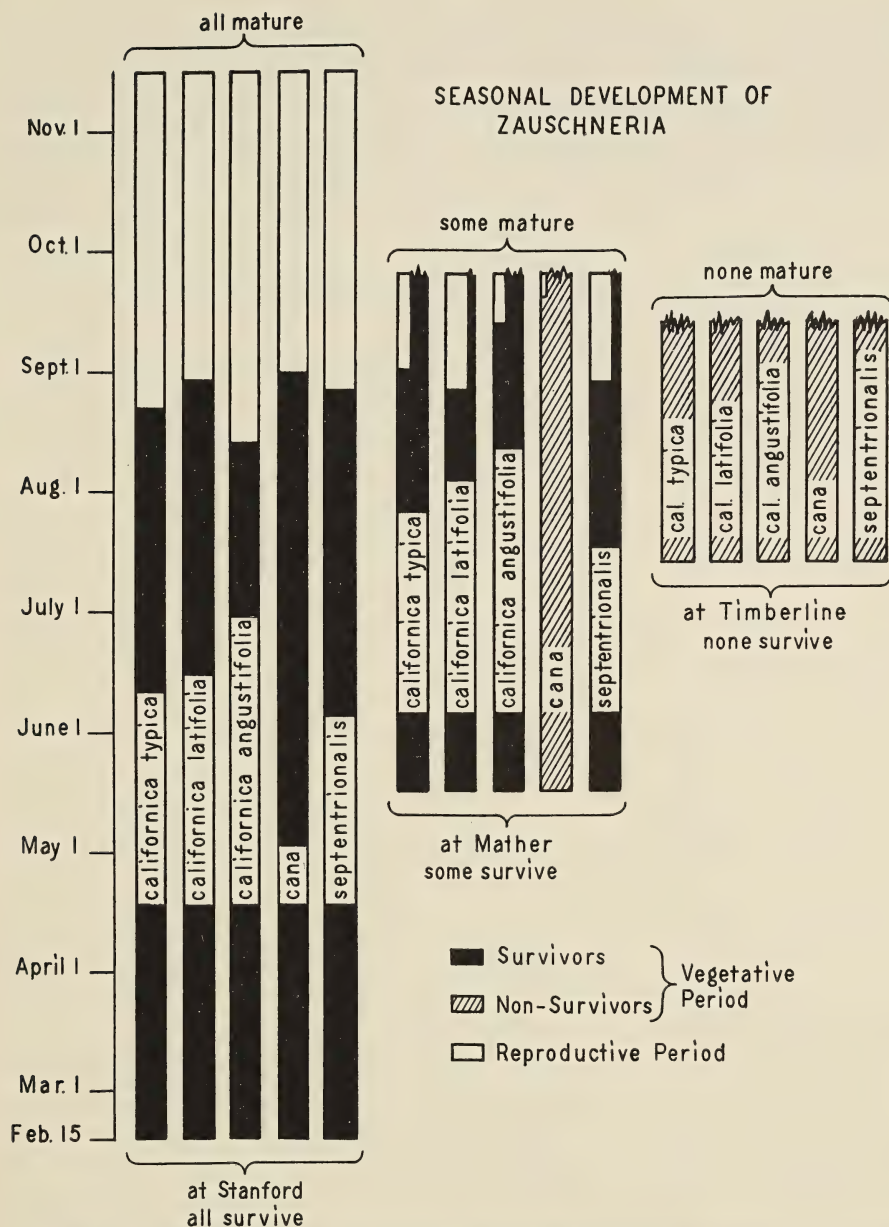


FIG. 87. Graph of seasonal development in clones representing ecotypes and ecospecies of *Zauschneria* at Stanford, Mather, and Timberline, expressed in terms of the time scale at left.

Constructed from data averaged during the years 1934 to 1937 for 35 individuals of *californica typica*, 42 of *californica latifolia*, 6 of *californica angustifolia*, 10 of *cana*, and 7 of *septrionalis*. See figures 91 and 92 for additional information concerning the individual plants represented in each group.

same time. The shortened vegetative period has resulted in a somewhat smaller plant, although this reduction in size is not at all in proportion to the reduction in the amount of time for growth. An exception to this reduction in size is *Z. californica latifolia*, which, in spite of the later start at Mather, produces stems quite as long as at Stanford and yet flowers on an average a few days earlier. This ecotype is native in the Mather region, a fact which is in keeping with its much greater efficiency at that station as compared with the forms from lower elevations.

Not all forms are able to hasten development at Mather to the same extent. As mentioned, *Z. cana* fails to reach the flowering stage in most years, but another diploid, *Z. septentrionalis*, reaches maturity about as consistently as the tetraploid *californica latifolia*, which indicates that the two diploids have very different seasonal requirements. The tetraploid *californica angustifolia*, on the other hand, matures with only slightly better success than *cana*. From this it is apparent that the latter two forms, both of the same geographical area, have deep-seated physiological similarities even though one has twice as many chromosomes as the other.

The extent of the modifications in time of flowering at Stanford and Mather is shown graphically in figure 88. The same plants were employed as in figure 87. This graph summarizes the ecotypical differences mentioned above. It differs considerably in appearance from previous graphs of earliness—a difference that may be connected with the shortening of the vegetative period at Mather. The crossing of the lines that connect average dates of first flowers at Stanford and Mather indicates that the forms have a differential speed of development at the two stations.

The slower development at Mather of the two coastal forms, *Z. cana* and *Z. californica angustifolia*, is indicated by the comparatively steep slope of their lines; also, they are rather parallel. *Zauschneria californica latifolia*, on the other hand, is even earlier at Mather than at Stanford, a demonstration of its speedy development at Mather. Also, it is two weeks later than *angustifolia* at Stanford, but almost three weeks earlier at Mather. *Zauschneria californica typica*, the morphological and altitudinal intermediate, is also intermediate in earliness at both stations. *Zauschneria septentrionalis*, also a plant of the Coast Ranges, parallels it in earliness.

It will be remembered that similar crossings of lines in earliness

graphs were observed between Coast Range and Sierran ecotypes of *Potentilla glandulosa* and between coastal and Sierran ecospecies of *Horkelia*, but none of them were quite as spectacular as these in *Zauschneria*. Reactional inversions of this sort are probably indications of differences in metabolic rate under varying environmental conditions.

ANNUAL VARIATION IN EARLINESS. Since most *Zauschnerias* are close to their threshold limits for completing the reproductive cycle at Mather, it is of interest to study the annual variations that occur

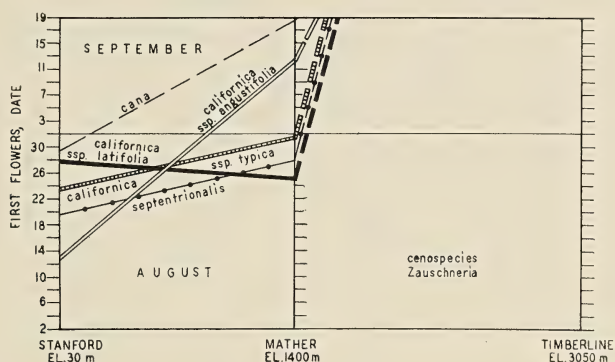


FIG. 88. Modification in dates of flowering in clones representing ecotypes and eco-species of *Zauschneria* at two altitudes.

Data averaged from the years 1934 to 1937 for the 100 plants indicated in figures 90 to 92.

in the date of appearance of the first flowers. Figure 89 summarizes the results from such a comparison. It is clear that 1934 and 1936 were late, while 1935 and 1937 were early. There is approximately a month's difference between the appearance of first flowers in the early and late years. This period is sufficient to determine whether or not many of the plants are able to produce ripe fruit.

It is shown in figure 88 that at Mather *Z. californica* ssp. *typica* flowered consistently five to ten days later than ssp. *latifolia*, the ecotype of higher elevations. This corresponds to the repeatedly observed tendency for *typica* to mature less successfully than *latifolia* at this station. Diploid *septentrionalis* follows the same general pattern as the others with different emphasis on the years. This difference in emphasis may be partly due to the smaller sample of individuals, but it probably indicates also that *septentrionalis* and

californica respond differently to the annual variations in the climatic complexes.

ZAUSCHNERIA AND POTENTILLA COMPARED AS TO SEASONAL REACTION. The pattern of yearly variation in earliness in the fall-flowering genus *Zauschneria* is just the opposite from that in the spring-flowering plants, *Potentilla glandulosa*, *P. gracilis*, and *Horkelia*. The years that are early for *Potentilla* at Mather are late for *Zauschneria*, and vice versa. This can be seen by comparing figures 30, 61,

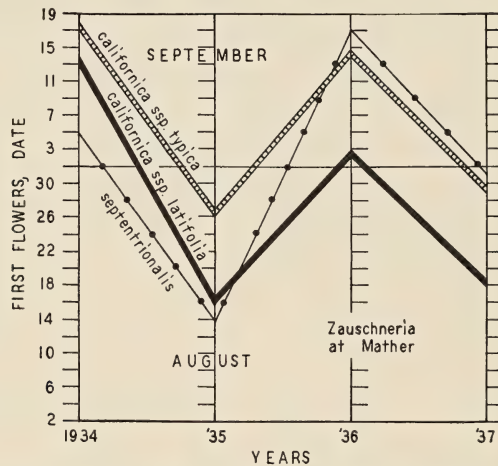


FIG. 89. Yearly variations in dates of flowering of *Zauschneria* at Mather.

The data are from observations on the same plants in four successive years; they are averaged from 34 individuals of *californica* ssp. *typica*, 42 of *californica* ssp. *latifolia*, and 7 of *septentrionalis*. See figures 91 and 92 for additional information concerning the individual plants within each group.

and 81 with 88, all constructed on data from Mather. Possibly the cause lies in the different modes of seasonal development in the groups. *Potentilla* and *Horkelia* are able to commence spring growth when the temperatures are still rather low, and their early flowering does not depend upon long-continued vegetative growth. Presumably they utilize the quantity of food materials stored in the fleshy root systems to accelerate spring development, so that they complete their reproductive cycle early. *Zauschneria*, on the contrary, is distinctly a warm-weather plant, and grows most vigorously in the hot summers that are not favorable for *Potentilla*. The flowering of *Zauschneria* appears to depend upon the organic materials produced during the same season, and its earliness upon the rapidity of

summer development rather than upon the earliness of the spring, as in *Potentilla* and *Horkelia*.

INDIVIDUAL VARIATION IN EARLINESS. The discussion in the preceding paragraphs has been simplified by considering the data from each of the taxonomic groups of *Zauschneria* as a unit. It should be emphasized that individual variations with respect to earliness, especially within *Z. californica* ssp. *typica* and ssp. *latifolia*, are conspicuous. Some examples are given in the accompanying tabulation.

PLANT NUMBER AND ORIGIN	DATE OF FIRST FLOWERS AT MATHER			
	1934	1935	1936	1937
<i>Zauschneria californica</i> ssp. <i>latifolia</i> :				
1028-1, San Jacinto Mts., Riverside Co. (early)	Aug. 15	Aug. 3	Sep. 15	Aug. 4
-7, Same (late)	Sep. 15	Aug. 25	Immature (no flowers)	Sep. 2
1074-2, Mineral King, Tulare Co. (early)	Aug. 20	July 19	Aug. 5	July 28
1065-1, Fallen Leaf Lake, Eldorado Co. (late)	Sep. 22	Sep. 6	Sep. 10	Aug. 25
Means for the subspecies, 43 plants	Sep. 13.2	Aug. 16.0	Sep. 2.5	Aug. 18.8
<i>Zauschneria californica</i> ssp. <i>typica</i> :				
1040-3, Paso Robles, San Luis Obispo Co. (early)	Aug. 7	July 25	Aug. 15	Aug. 3
1048-1, Coyote Creek, Santa Clara Co. (late)	Immature (no flowers)	Aug. 29	Immature (no flowers)	Aug. 30
1050-4, Alpine Creek, Santa Clara Co. (early)	Aug. 20	Aug. 4	Aug. 18	Aug. 15
1021-3, Lakeside, San Diego Co. (late)	Immature (no flowers)	Sep. 25	Immature (no flowers)	Sep. 5
Means for the subspecies, 38 plants	Sep. 17.5	Aug. 26.4	Sep. 14.4	Aug. 29.2

There are no such clear-cut correlations between earliness and altitude of original habitats as in *Potentilla glandulosa*; in fact, plants of *Zauschneria* from the same original habitat may show impressive individual variations, as for example the two plants of *latifolia* listed above from the San Jacinto Mountains. In ssp. *typica*, especially, there is no apparent correlation between individual variations and the character of the original habitats; but in ssp. *latifolia* early forms often come from higher elevations, such as at 2650 m. on Blue Ridge, San Antonio Mountains, at 2770 m. near Mineral King, and at 2700

m. in Tuolumne Meadows. These plants from high altitudes are generally more herbaceous and smaller than forms of the same subspecies from lower altitudes.

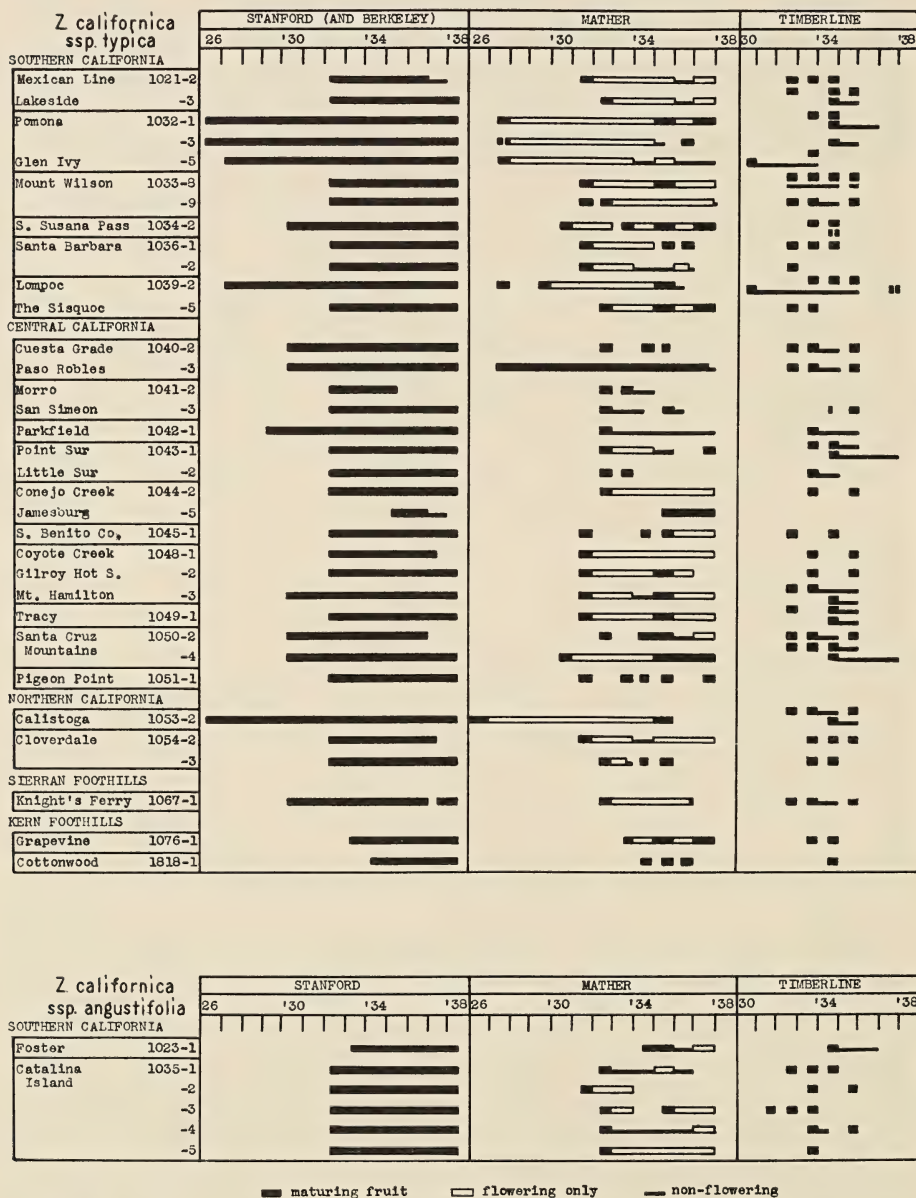


FIG. 90. Record of survival and flowering of clones of *Zauschneria californica* ssp. *typica* and *angustifolia* at three altitudes. The scale indicates years.

SURVIVAL. The survival of a plant or group of plants is closely allied to its seasonal development at the transplant stations. Some indication of the ability of the various forms to persist at the three stations has been shown in figure 87, in which all are represented as survivors at Stanford, all but *Z. cana* at Mather, and none at Timberline. These are the general conclusions, but the detailed analysis of the data shows that this classification into survivors and nonsurvivors is somewhat arbitrary.

TABLE 22
AVERAGE AGE OF ZAUSCHNERIA AT THE TRANSPLANT STATIONS

FORM	AT STANFORD				AT MATHER				AT TIMBERLINE			
	SURVIVORS		NONSURVIVORS		SURVIVORS		NONSURVIVORS		SURVIVORS		NONSURVIVORS	
	Av. age (mos.)	No. plants	Av. life (mos.)	No. trials	Av. age (mos.)	No. plants	Av. life (mos.)	No. trials	Av. age (mos.)	No. plants	Av. life (mos.)	No. trials
TETRAPLOIDS:												
<i>Zauschneria californica:</i>												
ssp. <i>angustifolia</i>	83.0	5		61.2	5	19.8	14		6.2	11
ssp. <i>typica</i>	91.9	30	60.0	7	66.6	29	23.7	45		10.6	86
ssp. <i>latifolia</i> ...	78.5	29	33.3	22	75.5	43	25.2	24	60.0	2	12.5	65
DIPLOIDS:												
<i>Zauschneria cana</i>	89.4	8	58.8	4		13.7	53		6.0	28
<i>Zauschneria septentrionalis</i> ...	52.3	3	29.9	6	49.8	6	15.8	12		7.8	13

This is evident in the graph of survival, figure 90. For example, nearly all transplants of *Z. californica typica* and *angustifolia* thrived and matured at Stanford, while they seldom matured at Mather, except 1040-3. At Timberline all failed.

The average ages of the plants now living, and the average length of life of those that died at the three stations, serve as an approximate index of survival. These are summarized in table 22, from which it is quite evident that life spans are longest at Stanford. This table shows no striking differences between the subspecies of *californica*, but closer study indicates that ssp. *latifolia* survives at least somewhat better at Mather than at Stanford, whereas the reverse situation holds for the other two. The higher percentage of nonsur-

vivors in *latifolia* at Stanford reflects the losses from diseases such as rust, and weakening by summer drought, to which it is more susceptible than other forms.

In comparing the survival record of *ssp. latifolia*, figure 91, with

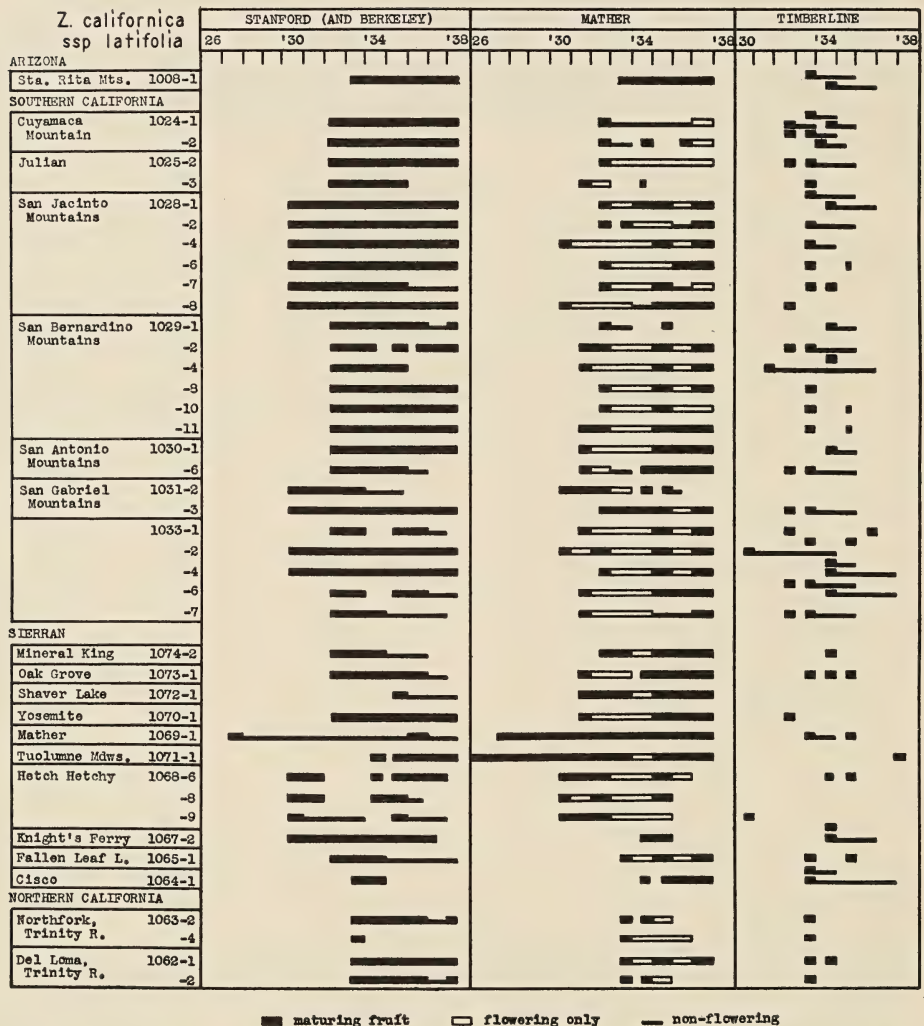


FIG. 91. Record of survival and flowering of clones of *Zauschneria californica* ssp. *latifolia* at three altitudes. The scale indicates years.

that of the other two subspecies in figure 90, it is seen that *latifolia* matures at Mather more frequently than *typica* or *angustifolia* and that it is more prone to remain vegetative at Stanford. At Timberline, *latifolia* survives a little better than any of the other *Zauschne-*

rias. A few hardy individuals have persisted in the slope garden for as long as five years, but in the meadow garden they have never survived more than one winter.

There is a distinct difference in survival between the tetraploid *californica* and the two diploid coastal species at Mather. The available evidence for the latter is summarized in figure 92. *Zauschneria cana* grows luxuriantly at Stanford but fails repeatedly at Mather. The four instances of flowering there did not result in ripe seed.

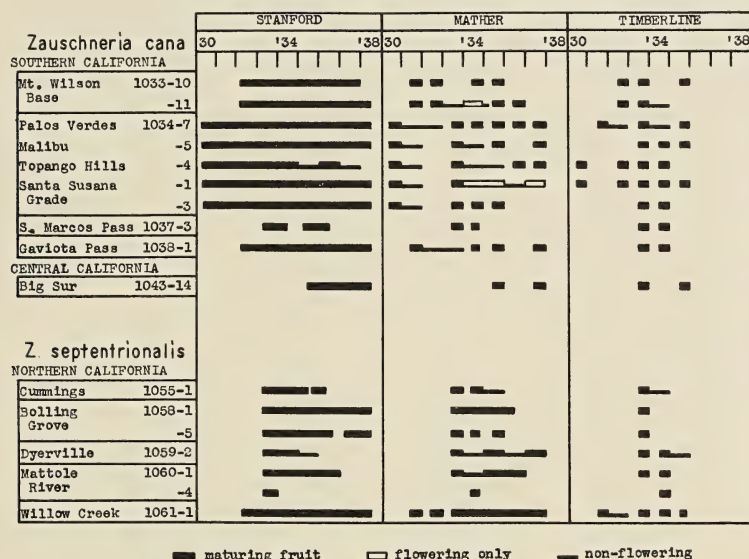


FIG. 92. Record of survival and flowering of clones of *Zauschneria cana* and *Z. septentrionalis* at three altitudes. The scale indicates years.

Zauschneria septentrionalis is definitely more successful at Mather, where it is able to mature seed although it does not flower every year. However, it does not succeed particularly well either at Stanford or at Mather.

Zauschneria has quite other survival boundaries than the *Potentilleae*. All *Potentillas* from low elevations were able to survive at Mather and produce ripe seed; even the coastal *Horkelias*, which were weakened there, managed to mature fruit. But Mather is definitely near the upper limit for the *Zauschnerias*. Even many members of the montane ecotype fail to mature seed there in certain years, and the coastal *Z. cana* survives as poorly at Mather as the Coast Range

ecotype of *Potentilla glandulosa* does at Timberline. The *Zauschnerias* appear to belong to a different and more southern floral element than the *Potentillas*, and the best ecotype they could develop for colder conditions is *Z. californica latifolia*.

MORPHOLOGICAL MODIFICATIONS

The modifications of morphological characters can best be described by first selecting representative examples of each ecotype for discussion and illustration. A brief, more general discussion will then follow.

Zauschneria cana grows very vigorously at Stanford, but rather weakly at Mather for a year or two before it dies, and only occasionally does it survive a winter at Timberline. The typical appearance of a clone of this species at Stanford, Mather, and Timberline is shown in figure 93. The specimen taken at Stanford is a typical woody stem as it appears at flowering time; clone members at this station develop a great many of these and form vigorous, semi-shrubby plants. These stems often live several years.

At Stanford, the plants of *cana* develop rootstocks in spring; they spread and colonize small areas, and give rise to new flowering stems, but also the old stems produce flowers. Leaves produced in spring are broader, longer, thinner, less pubescent, and less fascicled than those produced later in the season. The summer leaves are mostly fascicled and found on branchlets arising from the axils of spring leaves after the latter have been shed. (See the small spring shoot beside the mature flowering stem at Stanford in figure 93.) This leaf dimorphism, which changes the appearance of *cana* as the season progresses, suggests that spring and summer leaves may play a part in regulating the water economy of the plant during the relatively moist spring and the subsequent dry summers that characterize the climate to which *Z. cana* is naturally restricted.

At Mather, *Z. cana* scarcely reaches the mature-leaf stage by late September or early October, the end of the growing season. Flowers and seeds are very seldom developed, and stems do not become very woody, because, being winter-killed, they grow as annual shoots, originating each spring from the underground rhizomes. The plants lose much of their vigor after wintering, and frequently die during the spring as the young, tender shoots are repeatedly killed by late

May and early June frosts. No propagules of *Z. cana* have been kept alive at Mather for more than three years, and these were from one individual.

At Timberline, *Z. cana* usually dies the first winter after transplanting, but exceptionally well-established plants may survive as



FIG. 93. Modifications in a clone of *Zauschneria cana* at three altitudes.

This plant, 1033-11, was dug November 6, 1930, near the base of Mount Wilson, Los Angeles County, at 600 m.; $n=15$. The propagules at Stanford and Mather were planted in 1932, and the one at Timberline in 1933. The specimens were taken in 1934. Note the contrast between the mature foliage and spring leaves at Stanford, and the incomplete development of stems at Mather and Timberline.

long as two winters. The growth made by such plants during the short summers consists only of young vegetative shoots that become less than ten centimeters long, as shown in figure 93.

Zauschneria septentrionalis has not been so extensively transplanted as the other groups. In contrast to the woody *Z. cana*, it produces herbaceous stems that naturally die at the end of the growing season at Stanford as well as at Mather. Plants of *septentrionalis* do not suffer the same handicaps at Mather that *Z. cana* does through the winter killing of its aerial parts. They are stronger at Stanford, however, but do not really thrive at either station. The Stanford-grown plants are more glandular, have somewhat narrower leaves, longer stems, and more flowers, and are generally more robust than those at Mather. Other characters are but little modified, as evidenced in figure 94 (1060-1). In some forms of *Z. septentrionalis* the upper and lower leaves differ markedly in appearance because of the extensive development of a dense gray pubescence on the lower leaves of the plant. At Stanford, the lower canescent leaves outnumber the green upper ones, while at Mather the proportion may be reversed. Like all the other *Zauschnerias*, it produces only juvenile foliage at Timberline.

Zauschneria californica ssp. *angustifolia* reacts much like *Z. cana*, as is shown in figure 94 (1035-4). Its woody stems may persist for a second year at Stanford, but they are winter-killed and replaced by new shoots each spring at Mather, which gives it a more herbaceous appearance. The spring foliage of *angustifolia* consists of larger and greener leaves than those developed in summer. The summer leaves are more canescent, shorter, and narrower, and are prone to be clustered in fascicles in the axillary buds of the spring leaves. This dimorphism is similar to, but less pronounced than, that in *Z. cana*. At Timberline, *angustifolia* may occasionally survive one winter to produce juvenile shoots.

Zauschneria californica ssp. *typica* and ssp. *latifolia* grow with more vigor at Mather than any of the other groups in the genus; *latifolia* does the better of the two, but neither is modified very much. Typical aspects of these subspecies are shown in figure 95. The stems of *typica* are shorter at Mather than at Stanford, but *latifolia* is as tall or even taller at Mather. From oft-repeated observations in the transplant gardens, *typica* thrives better than *latifolia* at Stanford, while the reverse is true at Mather. Thus *typica* suf-

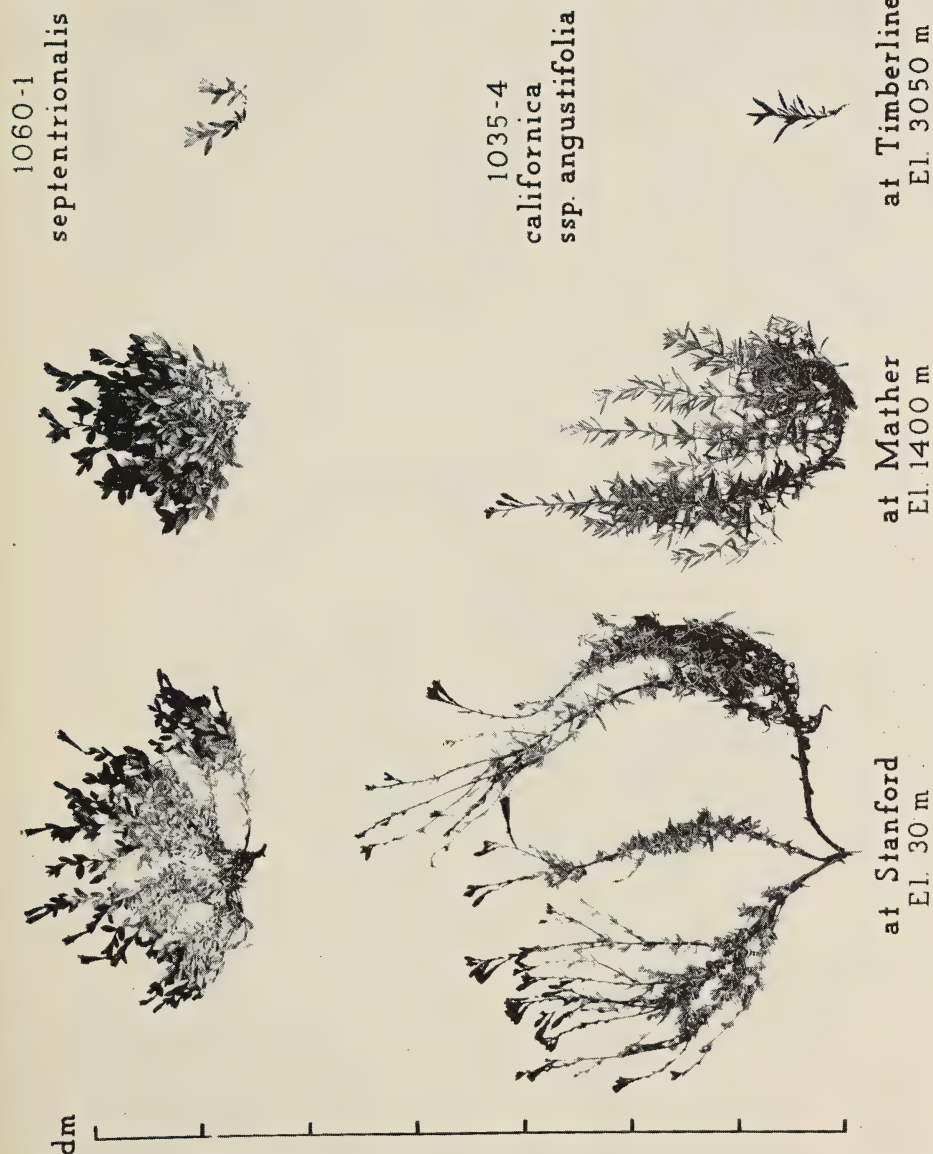


FIG. 94. Modifications in clones of *Zauschneria septentrionalis* and *Z. californica* ssp. *angustifolia* at three altitudes. Above: 1060-1, dug September 18, 1932, along the Mattole River near Petrolia, Humboldt County, at ca. 125 m.; $n=15$. Propagules were planted at Stanford and Mather in 1933 and at Timberline in 1934. Specimens taken at Stanford in 1936, at Mather in 1935, and at Timberline in 1934. Below: 1035-4, dug November 4, 1930, on Catalina Island, at 300 m.; pentaploid, $2n=ca. 75$. Propagules were planted at Stanford and Mather in 1932, and at Timberline in 1935. Specimens all taken in 1935.

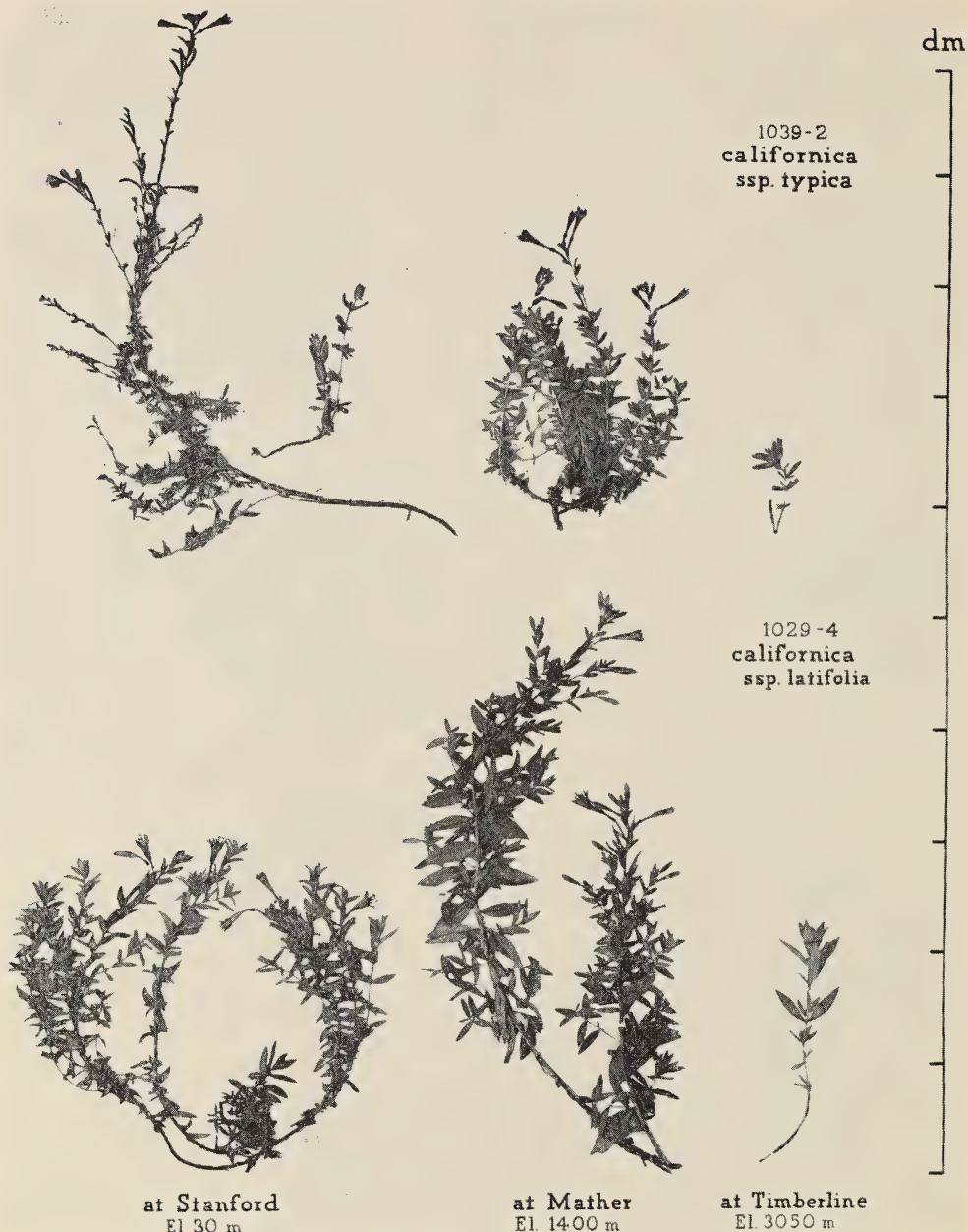


FIG. 95. Modifications at three altitudes in clones of *Zauschneria californica* sspp. *typica* and *latifolia*.

Above: 1039-2, dug April 10, 1926, near Lompoc, Santa Barbara County, at 200 m. The propagule to the left was grown at Berkeley from 1927 to 1929 and at Stanford from 1929; the other divisions were set at Mather in 1927, and at Timberline in 1930 from a Berkeley propagule. Specimens taken at Stanford and Mather in 1934, and at Timberline in 1935; the latter includes the entire growth made at the alpine station during the season. The five-year survival at Timberline is unusual.

Below: 1029-4, dug November 10, 1930, from above Mill Creek, San Bernardino Mountains, at 1450 m. The propagules were planted at Stanford in 1932, and at Mather and Timberline in 1931. Specimens taken at Stanford and Mather in 1935 and at Timberline in 1933.

fers less than *latifolia* from the dry summers and from diseases at Stanford; and *latifolia* resists the cold winters and the spring frosts at Mather better than *typica*.

The leaves of both *typica* and *latifolia* are widest at Mather. Some individuals of both subspecies are very glandular, exuding large quantities of resinous material from leaves and stems. The greater quantity is secreted at Stanford, apparently a result of the greater age attained there by the foliage.

Although such modifications take place, it is obvious from intense study of the transplants of *Zauschneria* that all plants retain their individual distinctions at the three stations. There is no evidence

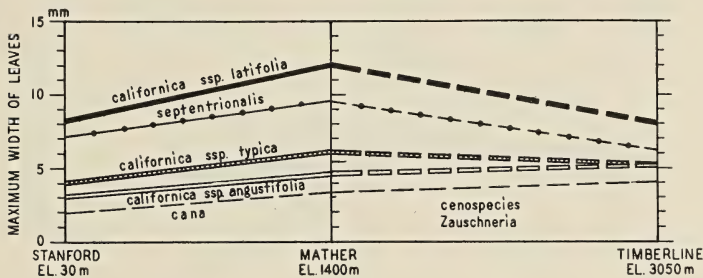


FIG. 96. Modifications at three altitudes in width of leaves in clones representing ecotypes and ecospecies of *Zauschneria*.

Data graphed are averaged from the years 1934 to 1937 for the 100 plants in figures 90 to 92.

whatever that the differences between any two subspecies or species have been erased by transplanting to another climate, or that minor genetic variants are changed into other forms. Transfer from one altitude to another changes vigor and appearance primarily because the mode of development is changed.

Two modifiable characters that prove to be good indicators of the extent of the changes are the maximum width of leaves of comparable age, and the length of stems. The modifications of leaf width are shown in the graph, figure 96. The leaves of all are widest at Mather, but they retain their relative differences. Lengths of stems of the same plants are shown in figure 97. It is evident that stem lengths are reduced at Mather in the three woody groups, *Z. cana*, *californica angustifolia*, and *californica typica*, whereas those with herbaceous stems show little difference at the two stations.

Spring shoots on propagules at Stanford are remarkably like those

produced at Mather and Timberline—so much like them, in fact, that they cannot be readily distinguished, although at the alpine station the internodes are somewhat shorter, the leaves smaller, and the foliage lighter green. This is illustrated in figure 98.

EFFECT OF LOCAL INFLUENCES. Most forms of *Zauschneria* are capable of exhibiting rather striking differences in appearance when grown in both sun and shade gardens at a given altitude. Shade causes the leaves to become larger, thinner, and less pubescent, and

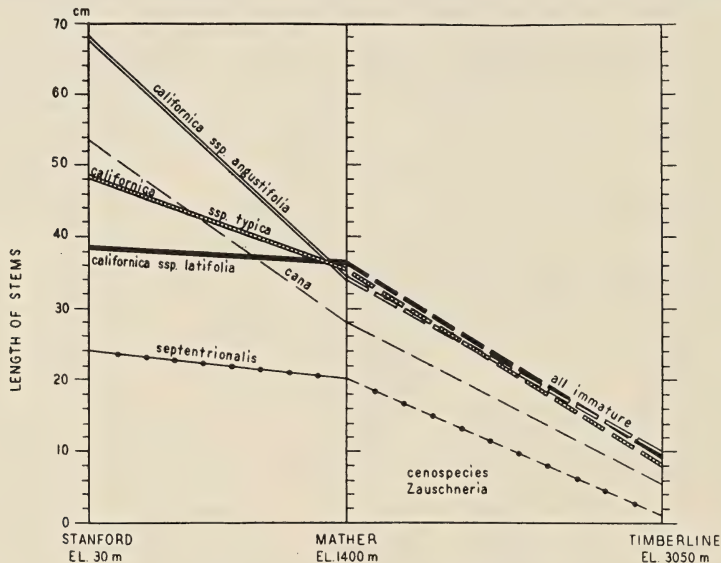


FIG. 97. Modifications at three altitudes in length of stems in clones representing ecotypes and ecospecies of *Zauschneria*.

Data from the same sources as in figure 96. The broken lines to Timberline indicate the failure of all groups to survive there; *Z. cana* fails also at Mather.

the internodes to become longer. Flowers tend to be fewer in number and of larger size, and in some forms their scarlet color is less intense. Too much shade prevents flowering altogether, and markedly reduces vegetative growth.

Widening of leaves in shade is a characteristic modification in the water-light gardens at Mather, as graphed in figure 99. The leaves are widest in the shade and narrowest in the sun. This modification is most striking in the three plants of *ssp. latifolia* and least in *Z. septentrionalis*.

Zauschnerias occur mostly in sunny, rocky places. It is not sur-

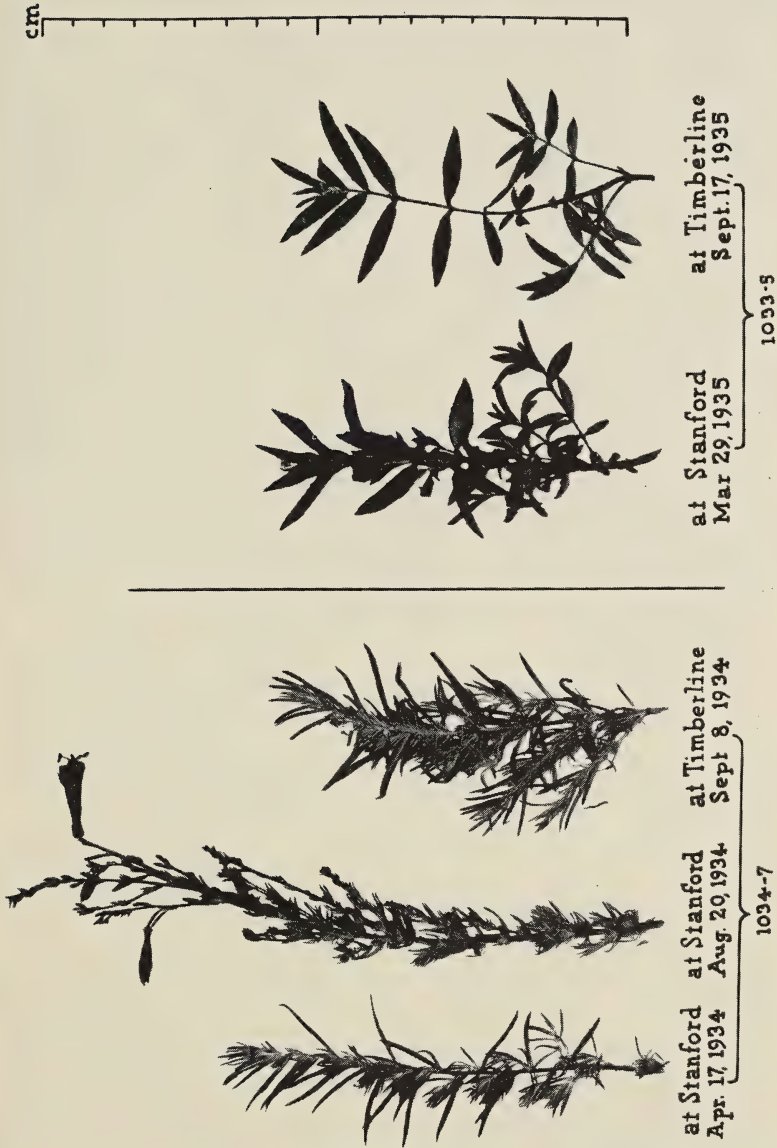


FIG. 98. Spring growth at Stanford compared with the season's growth at Timberline in clones of *Zauschneria*.
Left: branches of 1034-7, *Z. cana* from Palos Verdes, Los Angeles County, at Stanford in immature and mature stages, and at Timberline at the end of the growing season; set at Timberline one year previously.

Right: shoots of 1033-5, *Z. californica* ssp. *latifolia*, from Mount Wilson, Los Angeles County, at Stanford in spring growth, and at Timberline at the end of the growing season; set at Timberline slope garden four years previously.

prising, therefore, that plants in the dry sun garden at Mather, situated on a well-drained slope, thrive decidedly better, flower earlier, and produce more flowers than clone members in the moist sun garden, located in a meadow only a short distance away. Thus, local variations in habitat doubtless play an important rôle in the vigor and survival of these plants.

The effect of shade and altitude is immediately apparent upon the new tissues differentiating from the growing shoots. This is illus-

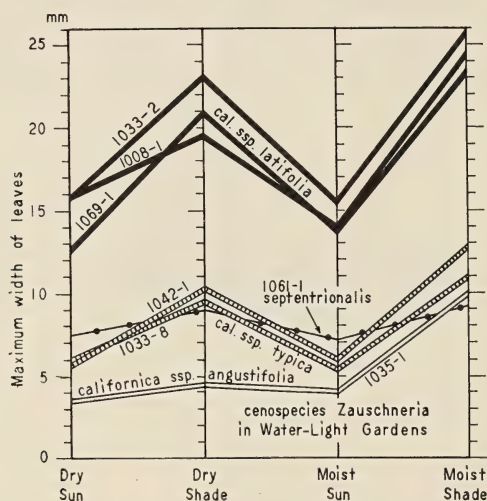


FIG. 99. Effect of the water-light gardens at Mather on width of leaves in clones representing four taxonomic groups of *Zauschneria*.

Data graphed are averaged from the years 1934 to 1937 for individual plants. See figures 90 to 92 for further information on the individuals represented.

trated in figure 100, 1039-2, showing a single branch of *Z. californica* ssp. *typica* which first grew in full sunlight at Berkeley, then was moved into the shade at Mather. For comparison, branches of forms differing genetically in leaf width, all grown in a uniform garden at Mather, are shown in the same figure (1121-3, 1129-11, and 1028-1). It is clear that the capacity of a given individual to modify the width of its leaves by the combined effect of shading and altitude may exceed hereditary differences between forms growing under uniform conditions.

The above illustration summarizes in very simple terms four important points concerning the modifications of quantitative characters in *Zauschneria*: (1) innumerable forms differing in heredity



FIG. 100. A modification compared with hereditary differences in leaf width in *Zauschneria californica*.

1039-2, branch of plant from 5 miles southwest of Lompoc, Santa Barbara County, at 200 m. The lower, small leaves were produced at Berkeley in the sun, while the upper, large ones appeared the same summer (1927) after the plant was moved into a garden at Mather densely shaded by pines.

The other three branches are from genetically different individuals growing in the uniform and sunny interstation garden at Mather, all collected the same season. Plant 1021-3 is a narrow-leaved ssp. *typica* from Lakeside, San Diego County, at 90 m.; 1029-11 is a more usual *typica* from the lower slopes of the San Bernardino Mountains, at 760 m.; and 1028-1 is ssp. *latifolia* from Mount San Jacinto, Riverside County, at 1370 m., all in southern California.

exist within each ecotype; (2) each individual has a certain capacity for adjusting or modifying itself to different conditions, such as to varying light intensity or moisture supply; (3) the modifications may simulate genetic differences in external appearance; and (4) the environmental effects, or modifications, are superimposed upon hereditary differences, and it is sometimes impossible to determine whether a given plant belongs to one subspecies or another if there is no evidence from cultural experiments. The operation of these interacting factors leads to the complex picture one sees in the many

kinds of variants in the field, or in the intergrades of a herbarium collection.

Characters which are especially modifiable in *Zauschneria* include size of leaves, density of pubescence, length of internodes, length of corollas, and habit of growth, all of which have been used as taxonomic characters in the genus. Density of pubescence is reduced by shading; when this is accompanied by increase in leaf width, lengthening of internodes, and an enlargement of flowers, as is usually the case, quite spectacular differences may be seen in clone members of the same individual that have merely been grown in full sunlight and in shade at a given altitude.

Despite the modificatory changes that may be induced in a given individual, it should be emphasized that its identity is never lost. The relative differences between any two genetic forms tend to be retained when both grow in the same gardens, although one form may show a greater degree of modification than the other. But throughout the process of transplanting, the genetic unity of every individual is preserved, and the capacity for variation is in itself a characteristic peculiar to the individual.

Turesson (1922*b*) has pointed out the parallelism between modification and hereditary variation in certain groups that he has investigated. In *Succisa pratensis*, for example, plants from exposed places in the salt meadows along the coast of Scania, Sweden, are dwarf. When transplanted into his garden at Åkarp, all plants became taller; but certain individuals, in the wild indistinguishable from others, were found to remain more dwarf than others from the same habitat. Of the taller forms, some were found to become as tall in cultivation as individuals originally from an inland swamp at Stehag whose heights in their native habitat were greater than those of any growing along the coast. Similar evidence is found by Turesson on habit characters of *Atriplex* and *Matricaria inodora*. Gregor (1930) has clearly shown the same principle in *Plantago maritima*, while other investigators, as discussed in chapter XI, have demonstrated it in other groups.

CYTOGENETIC INVESTIGATIONS

PURPOSE AND PRINCIPLES. The varied-environment experiments have given us a picture of the survival capacities of the different

groups of *Zauschnerias*, and of their modifications in different environments. The modifications are seen to be confined within the limits set by heredity. Transplanting to one or several uniform environments tells us whether or not two forms differ in heredity, but it tells little or nothing of the nature of their inherited characters, or of their systematic relationship. Since these must be determined in order to understand the nature of species, an extension of the investigations on *Zauschneria* into the fields of cytology and genetics was necessary.

Experiments by others and ourselves have shown that taxonomic relationship between forms is roughly proportional to their ability to exchange genes, either directly, or indirectly through an intermediary. The capacity for free interchange is expressed in the degree of fertility of the first generation, and in the vigor of the second generation. Because a difference in chromosome number often in itself constitutes a barrier to free interchange, a cytological survey of the genus is the first step in this investigation. Then follow systematic crossings among a group of key types carefully selected on the bases of morphology, geographic distribution, cytology, and reaction to transplanting. Fertility of the F_1 hybrids, behavior of the parental chromosomes in the F_1 , and vigor of the second generation are indicators of degrees of relationship to be weighed with evidence on morphological and ecologic-geographical differentiation.

The results from such an extended analysis in *Zauschneria* are shown in figure 101. This chart summarizes the results of the crossings and of other investigations that yield evidence on the degrees of genetic relationships. It is from this evidence that the taxonomic conclusions are drawn. These data, together with genetic analyses of plants from natural populations, provide the principal clues to phylogenetic relationships between the forms. Since seedlings of *Zauschneria* flower the same year that they germinate, and at the same time are perennial, the genus is well adapted for such genetic studies.

CYTOLOGICAL SURVEY. The somatic chromosome number of many *Zauschnerias* has been determined in roots. The list of the plants determined is given here for reference. The diagrams, figures 89 to 91, provide a key to the exact localities of most of the plants cited.

Z. cana; diploid, $n=15$:

San Gabriel Mountains: 1033-10 and -11. Southern California coastal: 1034-1, -3, -4, -5, and -7; 1037-3 and 1038-1. Santa Cruz Island: 2466-1.¹ Central California coastal: 1413-1 (near Big Sur, Monterey County).

Z. septentrionalis; diploid, $n=15$:

Eel River Basin: 1055-1; 1057-1 (Lane's Redwood Flat); 1058-2, -4, and -5 (Bolling Grove); 1059-1 and -2 (Dyerville). Mattole River Basin: 1060-1, -2, and -4. Trinity River Basin: 1061-1.

Z. Garrettii; diploid, $n=15$:

Salt Lake County, Utah: 1438-1 and -2.²

Z. californica typica; tetraploid, $n=30$:

Southern California: 1021-4 and -5 and 1025-1 (all San Diego County, coastal); 1033-8 and -9; 1034-2; 1036-1 and -2. Santa Cruz Island: 2467-1¹ (*villosa* Greene). Central California: 1048-1. Northern California: 1054-2. Interior foothills: 1076-1.

Z. californica angustifolia; tetraploid, $n=30$:

Southern California coastal: 1022-1 (La Jolla) and 1023-1. Catalina Island: 1035-1, -2, and -3.

Pentaploid, $2n = ca. 75$: 1035-4 and -5 (Catalina Island).

Z. californica latifolia; tetraploid, $n=30$:

Arizona: 1008-1. Southern California mountains: 1029-2; 1033-2 and -3 (Mount Wilson); 1031-1 and -3 (Barley Flats). Sierran: 1069-1 and 1074-2. Northern California: 1062-1 and 1063-2.

It should be mentioned that no *Zauschnerias* with $n=7$ or 8, as reported by Johansen (1929a, 1929b), have been found, nor any *californica typica* or *latifolia* with $n=15$ (Johansen, 1931). His counts of $2n=ca. 30$ for *microphylla* ($=cana$) and $n=30$ for forms of *californica* have been confirmed.

Zauschneria chromosomes are very small; the somatic ones are only about two microns in length, and the meiotic are about one micron in diameter. But the pollen mother cells are of exceptionally large size, fifty to seventy microns in diameter.

Meiosis still remains to be investigated thoroughly, but one of the tetraploid forms, 1035-1 (*californica angustifolia* from Catalina Island), has a varying number of quadrivalent chromosomes with zigzag chains and rings, although as many as 24 bivalents may occur.

¹ Plants kindly sent by Dr. Carl O. Wolf, of the Rancho Santa Ana Botanic Garden.

² From seeds generously supplied by Professor A. O. Garrett.

But even the diploid *cana* from Palos Verdes, 1034-7, had 10 pairs of chromosomes closely associated in five groups of 2 pairs each, while 5 single pairs were widely separated. The chromosome groups in *cana* showing parallel association were not true quadrivalents like those in *angustifolia*, but they suggest that even the diploid species of the genus may have a compound chromosome number.

Two pentaploid plants of *Z. californica angustifolia* ($2n=ca. 75$) were found in the central part of Catalina Island. They are less fertile than the tetraploid forms, and the extra 15 chromosomes distribute themselves unevenly during meiosis, although the pollen tetrads appear to be fairly regular and there is little evidence of elimination of chromosomes. A hexaploid form may therefore be expected to occur on the Island.

An interesting characteristic of *Zauschneria* is that the pollen grains stay together in tetrads until pollination. In genetic experiments it should therefore be possible to account separately for the exchange of genes that takes place in meiosis of each pollen mother cell.

CONSTANCY OF ECOTYPES ON SELFING. The three ecotypes or subspecies of the tetraploid *Z. californica* and the diploid species *Z. cana* and *septentrionalis* breed fairly true to type when self-pollinated, i.e., the offspring of one does not usually include segregants of another. The evidence for this is summarized below:

Zauschneria californica typica:

1033-8 (Mt. Wilson) selfed yielded.....	427 plants, all <i>typica</i>
1042-1 (Parkfield).....	530 plants, all <i>typica</i>

Zauschneria californica angustifolia:

1035-1 (Catalina Island).....	359 plants of <i>angustifolia</i> , and 11 plants of narrow-leaved <i>typica</i>
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Zauschneria californica latifolia:

1033-2 (Mt. Wilson summit).....	350 plants, all <i>latifolia</i>
1069-1 (Mather).....	20 plants, all <i>latifolia</i>

Zauschneria septentrionalis:

1061-1 (Willow Creek, Trinity R.).....	75 plants, all <i>septentrionalis</i>
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Zauschneria cana:

1033-11 (Mt. Wilson base).....	547 plants, all <i>cana</i>
1034-7 (Palos Verdes).....	303 plants, all <i>cana</i>

Zauschnerias are by no means homozygous, however, for all selfed populations show a wide range of variation. Almost all these selfed plants except 1033-8 throw lethals and sublethals, such as chloro-

phyll-deficient albinos, yellow-green plants, or slow-growing dwarfs. There are also numerous other variations in the degree of pubescence, height, and mode of branching, and minor variations in leaf width. Yet certainly neither *cana* nor *californica angustifolia*, both of shrubby habit, and with narrow, canescent leaves, produces herbaceous, broad-leaved forms with pilose pubescence. Likewise, broad-leaved *latifolia* does not segregate *typica*, with its lanceolate leaves of medium width, or vice versa. In other words, the taxonomic characters we have selected on the basis of their relative constancy in a geographical region prove to be relatively homozygous. This genetic evidence supports the value of these characters in taxonomy. It is to be expected that plants generally will prove to be so homozygous for taxonomically important characters of this type that, when inbred, they will reproduce their own kind only, and not their taxonomic relatives.

EFFECT OF INBREEDING. The presence of genes with lethal or sublethal effect is a common phenomenon in populations of habitually crossbreeding plants like *Zauschneria*, which is normally pollinated by humming birds. Almost all plants tested contained several recessive genes of sublethal effect, but no two of them appeared to contain identical lethals, for none of the twenty successful hybrid combinations listed in the crossing diagram (fig. 101) produced any sublethal or otherwise abnormal F_1 plants. Most races of *Zauschneria* suffer slightly by inbreeding, and some very much. For example, the Parkfield race of *californica typica* on selfing yielded a population of which only 8 per cent were fairly normal in vigor, and only 25 per cent survived the first year.

The Mather race of *Z. californica* ssp. *latifolia*, which produces very few offspring when selfed, is another example of the inbreeding effect. It is not very floriferous at Stanford, and when selfed, 50 per cent of its ovules abort, and but 10 per cent of its seeds germinate. Finally, only about 10 per cent of the seedlings obtained are vigorous enough to succeed fairly well. The inborn genetic weakness of the Mather and the Parkfield plants appears also in the second generation of their hybrids, which are weaker than those of other intraspecific hybrids. About 50 per cent of the ovules abort in many selfed tetraploid forms, another evidence of the frequency of lethal genes in natural populations of *Zauschneria*.

Vegetative propagation is probably widespread among *Zauschnerias*. Many of them occur beside streamways along which their stolons are carried by spring freshets. The Mather race, for example, appears to be very uniform and grows along the rocky, usually dry banks of a brooklet. Such vegetative propagation delays genetic selection and plays a rôle similar to that of partial apomixis.

CROSSING EXPERIMENTS. A series of thirteen different forms was selected for polygenic or diallel crossing. It represents the various morphologic and cytologic types from widely scattered and extremely different environments. At the time these forms were selected, little was known about their taxonomic status, because previous authors held conflicting views concerning the delimitation of species in the genus. Twenty-nine different hybrid combinations were attempted, six of which were unsuccessful. Among the twenty-three hybrids, six were completely sterile, six partially sterile, and one fertile hybrid yielded a weak second generation.

One cross produced a new, very fertile semi-allotetraploid form, and nine produced fertile hybrids with vigorous second generations and no chromosome duplication. These results, which are presented in a crossing polygon, figure 101, indicate that there are four freely interbreeding groups corresponding to the four species mentioned in the introduction to this chapter. The crossing polygon summarizes the results and the taxonomic conclusions drawn from them. A synopsis of the individual crossings is tabulated below.

ZAUSCHNERIA HYBRIDS

cana \times *cana* ($n=15 \times 15$):

- (1) 1034-7 (Palos Verdes) \times 1033-11 (Mount Wilson) and reciprocal:

81 F_1 plants and 542 F_2 , all *cana*. The fertility of F_1 was about 50 per cent and the germination 20 to 66 per cent. The harvest in F_1 represented about 2400 possibilities in the ovules, but of the 542 F_2 plants obtained, only 239 were successful, or about 10 per cent of the original possibilities.

cana \times *septentrionalis* ($n=15 \times 15$):

- (2) 1033-11 (Mount Wilson) \times 1061-1 (Willow Creek) and reciprocal:

76 F_1 plants and 457 F_2 plants, the latter produced from about 7000 potential ovules in F_1 . Fertility of F_1 was 5 to 50 per cent, and germination 13 to 56 per cent. The F_2 segregated 6 *cana*, 2 *septentrionalis*, and a complete series of intermediates. Twelve F_2 plants were successful

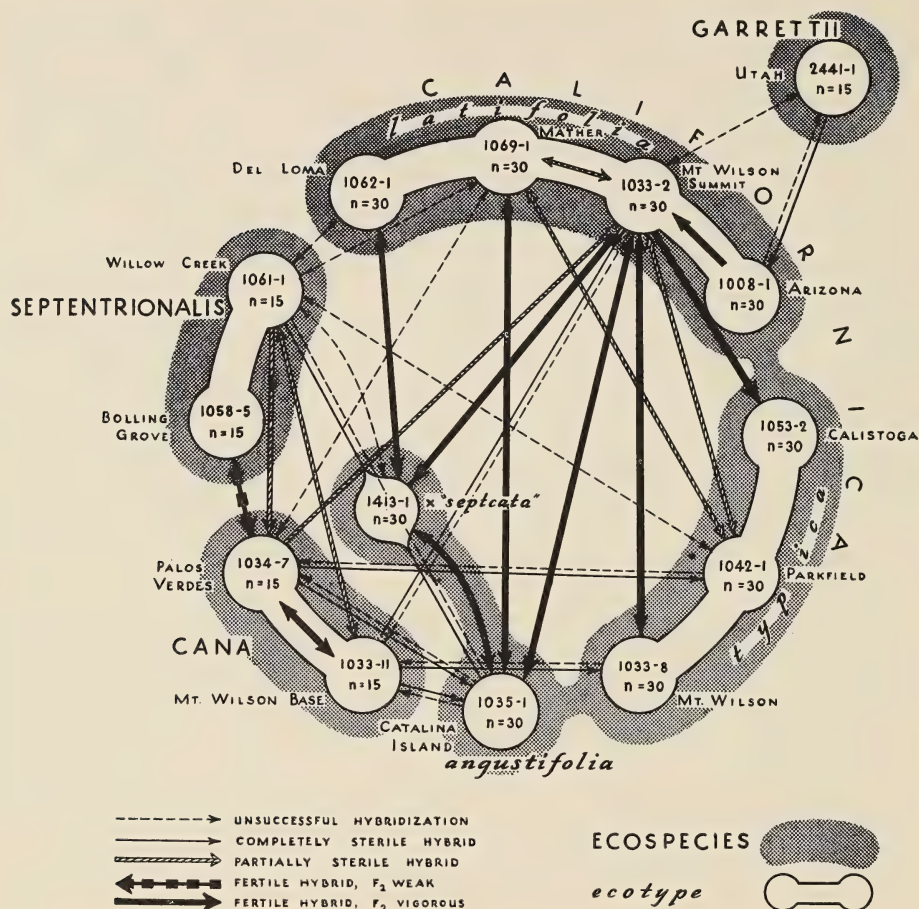


FIG. 101. Diagram summarizing the results of the crossing experiments in *Zauschneria*, with an interpretation of the degrees of relationship between the major groups.

Arrows indicate the direction the pollen was carried in crossing. See text for fuller explanation.

survivors, representing but 0.2 per cent of the original possibilities. The others were dwarfish or nonflowering and died mostly from attacks by rust.

- (3) 1034-7 (Palos Verdes) \times 1061-1 (Willow Creek), no reciprocal:
 35 F_1 plants and 361 F_2 , representing about 9000 of the original possibilities in the ovules. The fertility of F_1 varied between 1 and 50 per cent, germination between 4 and 25 per cent. The F_2 segregated 10 *cana*, no *septentrionalis*, but many intermediates and recombinations. Like the preceding culture, it contained many dwarf, weak plants that did not flower. These became badly infected with rust during the second year.

Only six F_2 plants were successful, or 0.066 per cent of the possibilities. Figure 102 illustrates the parents, an F_1 , and three F_2 plants.

- (4) 1034-7 (Palos Verdes) \times 1058-5 (Bolling Grove) and reciprocal:

129 F_1 plants, all weakened by attacks of mildew. Very fertile; 2133 F_2 plants were produced, but the cultures contained many dwarfish and weak plants like the other hybrids in this group. At the present writing this population is not yet mature, but 1232 plants have died and 621 more are weak, making a total of 1883 that may be classed as unsuccessful.

(NOTE ADDED IN PROOF: At the end of the 1939 season not one plant was successful. Those alive were either dwarfish, sick, or sterile; very few F_2 plants produced any seed whatever, probably on account of their weakened condition.)

californica angustifolia \times *cana* ($n=30 \times 15$):

- (5) 1035-1 (Catalina) \times 1033-11 (Mount Wilson):

3 F_1 plants, all sterile.

- (6) 1035-1 (Catalina) \times 1034-7 (Palos Verdes):

4 F_1 plants, all sterile. The two reciprocals of crosses 5 and 6 were unsuccessful.

californica typica \times *cana* ($n=30 \times 15$):

- (7) 1033-8 (Mount Wilson) \times 1033-11 (Mount Wilson base):

11 F_1 plants, all sterile.

- (8) 1042-1 (Parkfield) \times 1034-7 (Palos Verdes):

2 F_1 plants, both sterile. The two reciprocals of crosses 7 and 8 were unsuccessful.

californica latifolia \times *cana* ($n=30 \times 15$):

- (9) 1033-2 (Mount Wilson summit) \times 1033-11 (Mount Wilson base), with an unsuccessful reciprocal:

12 F_1 plants, all sterile.

- (10) 1033-2 (Mount Wilson summit) \times 1034-7 (Palos Verdes), with an unsuccessful reciprocal:

8 F_1 plants, sterile by self-pollination, but slightly fertile by open pollination. The F_1 crossed with 1035-1 (Catalina) produced 5 offspring, which yielded 56 progeny by open and self-pollination. All together, 72 offspring were obtained from this hybrid, all of which were of the tetraploid type, like *californica typica* or *angustifolia*. Although not very fertile, 39 were healthy, vigorous plants. All successful progeny contained at least one specifically pure genom.

- (11) 1069-1 (Mather) \times 1034-7 (Palos Verdes) and reciprocal:

Unsuccessful.

septentrionalis \times *californica angustifolia* ($n=15 \times 30$):

- (12) 1061-1 (Willow Creek) \times 1035-1 (Catalina), with an unsuccessful reciprocal:

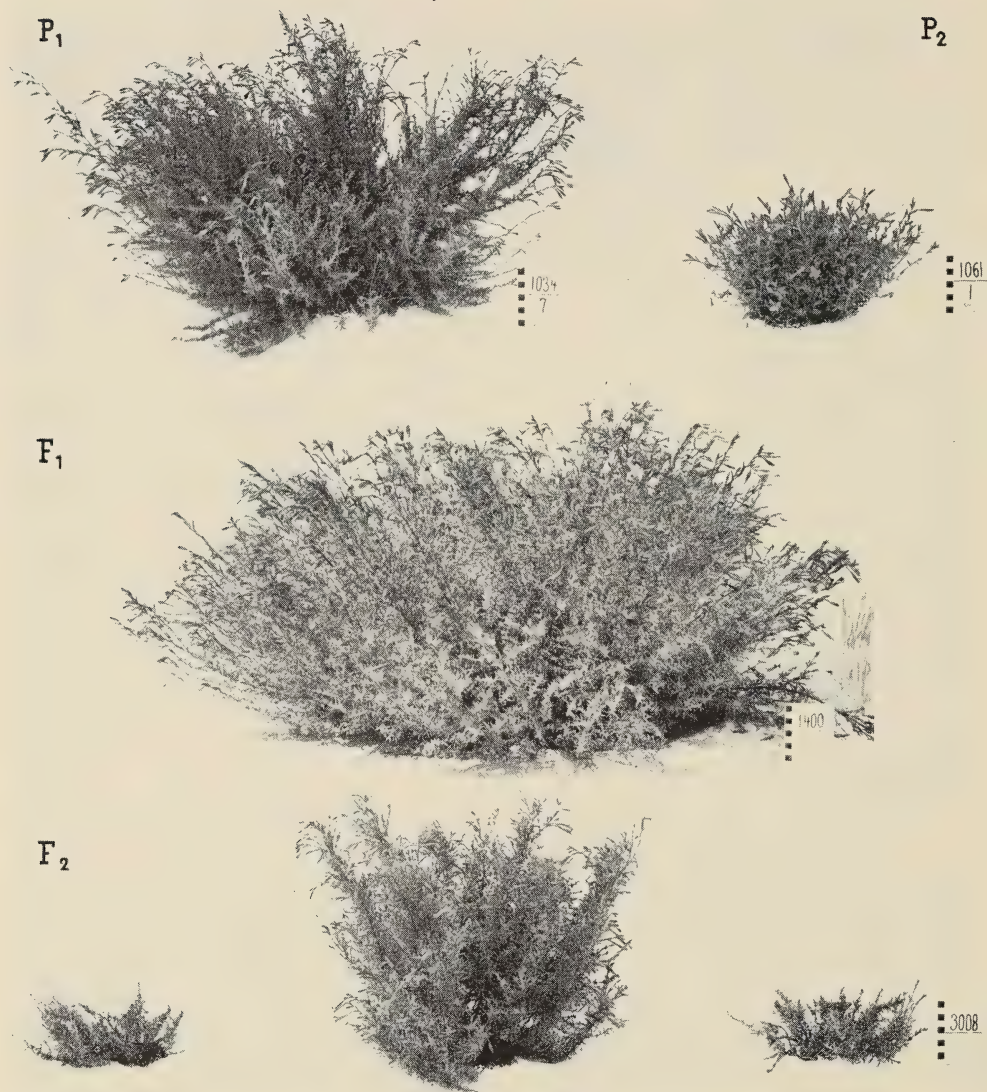


FIG. 102. An experiment in crossing two diploid ecospecies of *Zauschneria*.

Above: the parents, 1034-7, *Z. cana*, from near Palos Verdes, Los Angeles County, and 1061-1, *Z. septentrionalis* from Willow Creek, Humboldt County; each has 15 pairs of chromosomes. Center: their F_1 hybrid. Below: three two-year-old F_2 plants, a vigorous individual in the center (the strongest of 362 plants), the others weak and subnormal, like the majority of this population. The photographs are to the same scale, and were taken at Stanford.

2 F_1 plants obtained, which were assigned the numbers 1413-1 and -2. These were very fertile and tetraploid ($2n=60$). Unexpectedly, the hybrid was here obtained on the diploid as the maternal parent, and the chromosome number was 15 more than expected. Most likely, therefore, it originated from diploid ovules of *septrionalis* fertilized by normal pollen of *angustifolia*. The F_1 hybrid was more fertile (50 to 80 per cent) than most plants from natural habitats, and the seeds likewise germinated better (50 to 60 per cent). The F_2 consisted of 1174 plants, all similar to the F_1 , woody, and with narrowly lanceolate, silvery-canescant leaves; 678 of the F_2 were successful (equal to fully 22 per cent of the original possibilities from the ovules). For convenience, this new, fertile, relatively constant, semi-allotetraploid form with two genomes of *septrionalis* and one of *californica angustifolia* has been given the name "*septricata*" (from *septrionalis* \times "Catalina"). Further crossing tests indicate that "*septricata*" belongs to the species *Zauschneria californica* (cf. crossings 26-29). Figure 103 shows "*septricata*" and its parents.

californica typica \times *septrionalis* ($n=30 \times 15$):

- (13) 1042-1 (Parkfield) \times 1061-1 (Willow Creek) and reciprocal:
Unsuccessful.

californica latifolia \times *septrionalis* ($n=30 \times 15$):

- (14) 1069-1 (Mather) \times 1061-1 (Willow Creek) and reciprocal:
Unsuccessful.
(15) 1062-1 (Del Loma) \times 1061-1 (Willow Creek) and reciprocal:
Unsuccessful.

californica latifolia \times *Garrettii* ($n=30 \times 15$):

- (16) 1008-1 (Arizona) \times 2441-4 (Utah), with an unsuccessful reciprocal:
4 F_1 plants, all sterile.
(17) 1033-2 (Mount Wilson summit) \times 2441-1 (Utah) and reciprocal:
Unsuccessful.

californica angustifolia \times *californica latifolia* ($n=30 \times 30$):

- (18) 1035-1 (Catalina) \times 1033-2 (Mount Wilson summit) and reciprocal:
116 F_1 plants, all referable to *californica typica*, about 75 per cent fertile. An average germination of about 50 per cent produced 3100 F_2 plants. Of these, 3091 were *californica typica* of various descriptions, only 9 (all from one small culture) could be classified as *latifolia*, and none were canescant or narrow-leaved like the *angustifolia* parent. There were 1296 successful plants, equal to about 14 per cent of the possibilities in the 9000 original ovules.
(19) 1035-1 (Catalina) \times 1069-1 (Mather) and reciprocal:
74 F_1 plants similar to *californica typica*, about 40 per cent fertile. A germination of about 10 per cent yielded 669 F_2 plants, of which 350

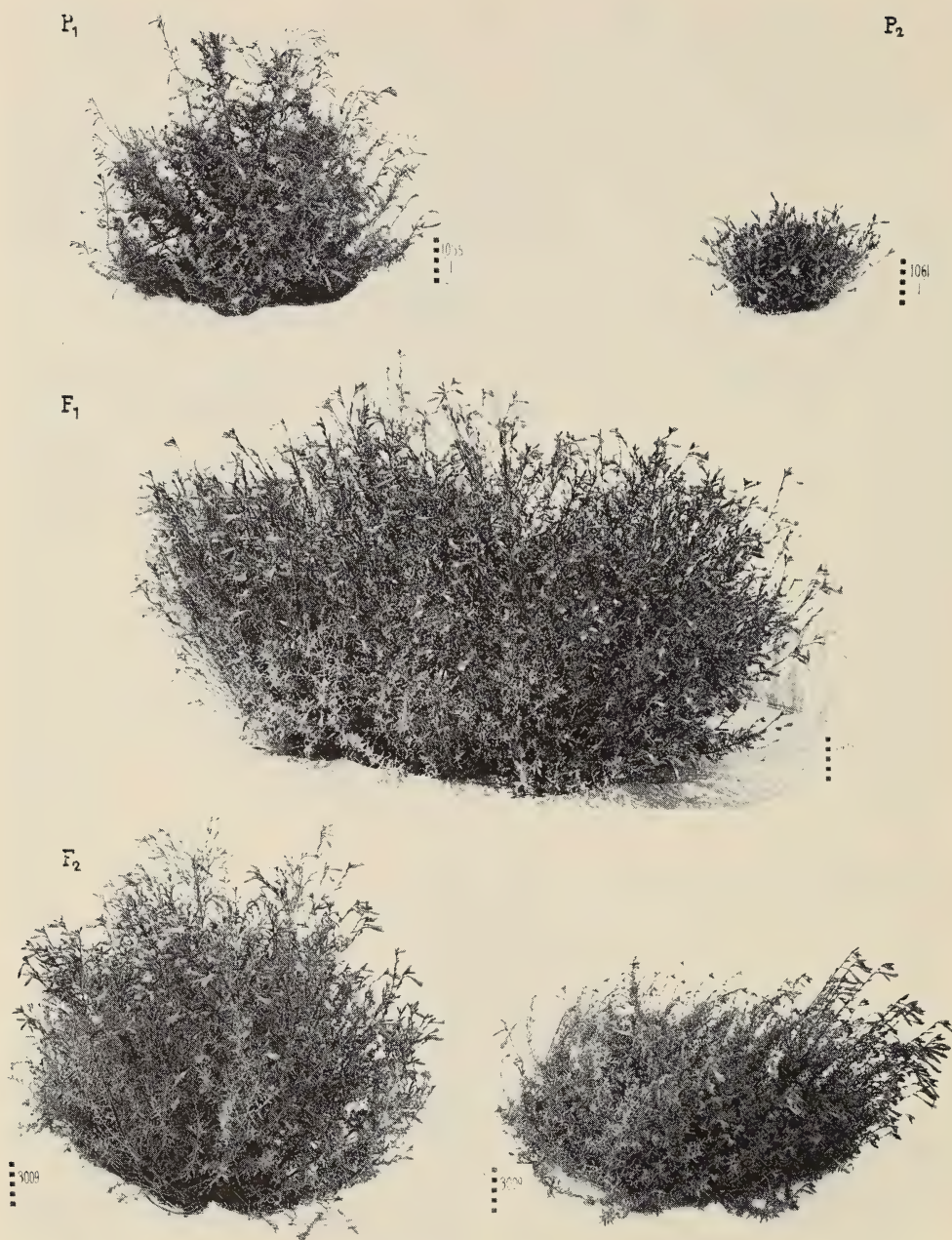


FIG. 103. History of a semi-allopolyploid, *Zauschneria* "septicata."

Above: the parents, 1035-1, *Z. californica* ssp. *angustifolia* from Catalina Island, Los Angeles County ($n=30$), and 1061-1, *Z. septentrionalis* from Willow Creek, Humboldt County ($n=15$). Center: an F_1 offspring, a semi-allopolyploid, $2n=60$. Below: examples of two-year-old F_2 plants; the entire population consisted of vigorous individuals like these, similar to the F_1 . The photographs are to the same scale, and were taken at Stanford.

appeared successful after two years. They were classified as 444 *californica typica* (13 of which were gray-canescens like the *angustifolia* parent, the others greenish), 9 *latifolia*, and none of true *angustifolia*.

californica typica \times *californica latifolia* ($n=30 \times 30$):

- (20) 1033-8 (Mount Wilson) \times 1033-2 (Mount Wilson summit) and reciprocal: 86 F_1 plants as fertile as plants from natural populations; 25 to 50 per cent of the seeds germinated, producing 293 F_2 plants, all *californica typica*, but some approaching *latifolia* in width of leaves. Of these, 158 were successful survivors at Stanford.
- (21) 1042-1 (Parkfield) \times 1033-2 (Mount Wilson summit) and reciprocal: 96 F_1 plants, about 40 per cent fertile; the seeds, of which 25 to 40 per cent germinated, produced 233 F_2 plants, 32 of which were successful. Four or five F_2 plants approached *latifolia* in width of leaves, but all the others were *californica typica* of varying leaf width.
- (22) 1042-1 (Parkfield) \times 1069-1 (Mather) and reciprocal: 46 F_1 plants, all rather sterile. With a germination of about 20 per cent, 26 F_2 plants were produced, 5 of which were classified as *californica latifolia* and 21 as broad-leaved *californica typica*, all successful.
- (23) 1053-2 (Calistoga) \times 1033-2 (Mount Wilson summit), the reciprocal not attempted:
5 F_1 plants, as fertile as plants from natural populations. A total of 156 F_2 plants were grown, segregating forms varying from *californica typica* to *latifolia* and many intermediates. All appeared healthy and vigorous during the first year, after which they were discarded.

californica latifolia \times *californica latifolia* ($n=30 \times 30$):

- (24) 1033-2 (Mount Wilson summit) \times 1069-1 (Mather) and reciprocal: 15 F_1 plants, about 40 to 80 per cent fertile, but only 4 per cent of their seeds germinated for the F_2 . The flowering of F_1 was not strong. The F_2 consisted of only 105 plants, of which 42 were successful. Remarkably enough, this combination segregated *californica typica*. There were 33 referable to *latifolia* and 27 to *typica* in a population of 60 plants.
- (25) 1033-2 (Mount Wilson summit) \times 1008-1 (Arizona), the reciprocal not attempted:
22 F_1 plants, as fertile as plants from natural populations. Their seed germinated well, and of 1284 F_2 plants produced, all were referable to *californica latifolia*. Only 298 of these plants were unsuccessful and the cultures are vigorous and healthy. This makes *Z. arizonica* conspecific with *Z. californica*.

californica "septcata" \times *septentrionalis* ($n=30 \times 15$):

- (26) 1413-1 ("*septcata*") \times 1061-1 (Willow Creek) and reciprocal:
Unsuccessful. This is a backcross of "*septcata*" to its maternal parent.

californica "septcata" \times *californica angustifolia* ($n=30 \times 30$):

(27) 1413-1 ("septcata") \times 1035-1 (Catalina) and reciprocal:

This backcross of "septcata" to its paternal *angustifolia* parent produced an F_1 consisting of 60 uniform plants that were almost indistinguishable from *angustifolia* except that the leaves were slightly wider. If the theory of the origin of "septcata" is correct (see cross 12), this hybrid should contain 45 chromosomes of *angustifolia* and only 15 of *septrionalis*. It was as fertile as the most fertile forms from natural populations, for 60 to 90 per cent of its seeds germinated. The F_2 consisted of 2245 plants, of which 422 were unsuccessful during the first year. All were canescent like both grandparents. The F_2 plants were classified by leaf width as 2223 *californica angustifolia* and 18 *californica typica* but canescent. None had leaves nearly as wide as any form of *septrionalis*. Five plants had white flowers, of which three had empty anthers. To our knowledge these are the first white-flowered *Zauschnerias* produced.

californica "septcata" \times *californica latifolia* ($n=30 \times 30$):

(28) 1413-1 ("septcata") \times 1062-1 (Del Loma) and reciprocal:

F_1 consisted of 52 plants, that were broad-leaved and low, varying from *californica latifolia* to broad *typica*. The general impression was that of a population of *latifolia* that contrasted markedly with the shrubby, canescent, narrow-leaved plants of the preceding cross. Reasoning from the supposed origin of "septcata" (see cross 12), the chromosomes of this hybrid should consist of 15 from *angustifolia*, 15 from *septrionalis*, and 30 from *latifolia*. If the genom of *septrionalis* is essentially the same as one-half of a genom of *latifolia*, the preponderant influence of *latifolia* in this hybrid is easily understood. The fertility and germination of seed was even better in this than in the preceding hybrid. The F_2 consisted of 2658 plants, of which only 292 were unsuccessful the first year. Almost all the F_2 plants were low and similar to *latifolia*, but they varied in width of leaves from the broad, oval *latifolia* type to the lanceolate forms of *typica*, none being as narrow as *angustifolia*. Most plants were gray-pilose with a few as greenish-pilose as *latifolia*, while others were as gray-canescens as "septcata." This suggests that the chromosomes of all four sets of 15 are so homologous that they are partially interchangeable in this hybrid.

(29) 1413-1 ("septcata") \times 1033-2 (Mount Wilson summit) and reciprocal:

148 F_1 plants similar to those of the preceding cross, but taller with slightly narrower leaves. The fertility of the ovules was 30 to 60 per cent, but the viability of F_2 was not tested.

CONCLUSIONS ON RELATIONSHIPS. These breeding tests show that, in spite of relatively high interfertility, the two diploid species, *Z. cana* and *Z. septrionalis*, cannot freely exchange their genes in all

proportions without detriment to the offspring (see fig. 102). The exchange results in slow-growing and dwarf, rust-susceptible, or otherwise weak offspring. These species are, therefore, two distinct ecospecies of one cenospecies.

The tetraploids do not easily cross with the diploids, probably because of the differences in chromosome number rather than because of a great phylogenetic difference. This interpretation is reached from a study of the artificially produced "*septicata*," shown in figure 103. The increased number of chromosomes immediately created a barrier between it and its maternal parent, but enabled it to exchange genes freely with all other tetraploid forms.

The three tetraploid units, *californica angustifolia*, *typica*, and *latifolia*, are ecotypes of one ecospecies, namely, a coastal, a Coast Range, and a mid-altitude ecotype, respectively. They each fit a different environment, but readily exchange their genes. There are three apparent exceptions to free interchange of genes between the three ecotypes; they involve *californica typica* from Parkfield and *californica latifolia* from Mather. However, as previously mentioned, both of these plants abounded in sublethals. When their F_1 's are selfed, which would rarely happen in nature in this genus, the recessive sublethals become released from the influence of their dominant alleles, and this results in weak offspring similar to that of interspecific hybrids. Also, the Mather plant, as shown in the chart (fig. 101), is linked with the others through an intermediary with which it is interfertile.

The three ecotypes are morphologically recognizable, inhabit climatically different territories, and are physiologically different in their reactions, as shown in the transplant experiments. These are the criteria by which ecotypes are recognized. Where they meet in nature, hybrid recombinations are in evidence.

All *Zauschnerias* thus form one species complex, or cenospecies, which consists of three local diploid and one widely distributed and very variable tetraploid ecospecies. One might be tempted to consider the tetraploid *Z. californica* to be a cenospecies in itself, distinct from the diploid complex, if cross 10 had not shown that genes from *Z. cana* could be absorbed into the tetraploid, and if "*septicata*" (cross 12) had not proved that both genomes of *Z. septentrionalis* could become absorbed into *californica*. Subsequent crosses redistribute the chromosomes and genes of *septentrionalis* to various forms of

californica, thus creating increased variation in this species without any detriment to the offspring. This experiment opens a new possibility for explaining what may have happened in nature several times during the evolution of this and other genera.

Semi-allopolyploid hybrids similar to "*septicata*" have previously been reported in *Gossypium* (Skovsted, 1934) and in the cross *Zea Mays* \times *Euchlaena perennis* (Collins and Longley, 1935). A preliminary note on "*septicata*" has already been published (Clausen, Keck, and Hiesey, 1934, p. 177). In all of these, the diploid ovule originated from the diploid parent and the cross resulted in a cytologically balanced tetraploid form. In the sesquiploid hybrid of *Nicotiana Tabacum* \times *glauca* described by Webber (1930), the diploid ovule came from the tetraploid parent and resulted in a cytologically unbalanced hybrid with 24 pairs and 12 single chromosomes.

PROBABLE ORIGINS OF THE ECOTYPES OF *Z. CALIFORNICA*. It is tempting to venture into phylogenetic speculation in a genus of limited size like *Zauschneria*, in which so much is known of the distribution and reaction of ecotypes and ecospecies, and of their cytogenetic characteristics. The fact that even with this evidence the relationships can be determined only up to a certain point, leaving the larger question of origins still unanswered, impresses the need of great care in applying the phrase "phylogenetic concept of species" where no experimental evidence is at hand. It shows also that any system built upon speculative phylogeny must necessarily rest on a very uncertain foundation.

It is suggestive that each of the two distinct coastal diploid species has a geographical and morphological tetraploid counterpart. *Zauschneria cana* has its counterpart in *Z. californica angustifolia*, the two occupying much the same territory. If *angustifolia* is an autotetraploid *cana*, this would explain the constancy of "*septicata*" (cross 12). Likewise, *Z. septentrionalis* has its counterpart in *Z. californica latifolia*. Today, in the Trinity River Canyon, they grow no more than thirty kilometers apart. We might expect *latifolia* to have arisen by doubling of the chromosomes (autotetraploidy) of a green-leaved form of *septentrionalis*, representatives of which are almost indistinguishable from some forms of *latifolia*. The origin of "*septicata*" indicates that diploid gametes with 30 chromosomes occasionally occur in *septentrionalis*.

It seems natural to assume that *Z. septentrionalis*, from the moist, cool Redwood region, would give rise to an ecotype like *Z. californica latifolia*, which is associated with the moister and cooler regions. As is seen in the transplant experiments, *septentrionalis* thrives better at Mather than *cana*, which is likewise diploid, and even somewhat better than the tetraploid *angustifolia*. Nevertheless, if *septentrionalis* is the predecessor of *latifolia*, the equilibrium between the genes determining the physiological reactions must have been such that when all were duplicated, the ecologic range of the new species was changed, permitting it to migrate inland and to higher elevations. The new environment, favoring differential selection, and the increased possibility for variation as a tetraploid would account for the origin of morphologic races that mark some forms of *latifolia* as being very different from forms of *septentrionalis*.

Another possibility exists for the origin of *Z. californica latifolia*. The diploid *Z. Garrettii* of Utah is so similar to some of the tetraploid *latifolias* from the drier regions that they are almost indistinguishable. Today the two species are fairly well separated geographically, but if *Garrettii* had had a wider distribution in past ages, a form of *latifolia* might have arisen from *Garrettii* by autotetraploidy. In fact, there actually are two fairly well separated groups in ssp. *latifolia*: one in northwestern California and another in the drier southern half of the state and in Arizona, New Mexico, and Sonora.

It is likewise interesting that crossings between the supposed autotetraploids, *Z. californica angustifolia* and *latifolia*, produce a fertile and compatible hybrid very similar to *californica typica*. It is still more suggestive that this hybrid very rarely segregates either of its parents, but re-creates the entire variation characteristic for *californica typica* (crosses 18 and 19). Under normal conditions one would expect at least an indication of either the narrow leaves or the canescent pubescence of the *angustifolia* parent among 3100 F₂ plants, but such forms were not segregated. However, if *angustifolia* and *latifolia* are autotetraploids, just the condition found would be expected. The formula for a gametic set of chromosomes would be 15A + 15A for *angustifolia* and 15L + 15L for *latifolia*. In their hybrid the *angustifolia* and *latifolia* chromosomes would be expected to conjugate independently as follows: $\frac{15A}{15A} + \frac{15L}{15L}$. This would cause the two sets of *angustifolia* and the two of *latifolia* to exchange independ-

ently of each other and tend to reproduce the F_1 , which is morphologically indistinguishable from *californica typica*. In other words, *Z. californica typica* becomes a sort of delayed amphidiploid, produced via the autotetraploid stage from two morphologically and ecologically very different diploid species.

Another possibility, however, has to be considered for the origin of *Z. californica typica*. Cross 24 (*latifolia* from Mount Wilson \times *latifolia* from Mather) segregated *californica typica* in the F_2 . This indicates that the two broad-leaved parents had different genes for leaf width. Incidentally, plants with unusually wide leaves appeared also in this cross. But it appears ecologically more probable that the Coast Range ecotype arose from crossings between a montane and a coastal ecotype than from segregations in races belonging to the montane ecotype. The montane and coastal ecotypes come close together in southern California, and humming birds could carry the pollen over some distance. The reactions diagrammed in figures 88, 96, and 97 show that *californica typica* is remarkably intermediate between *latifolia* and *angustifolia* in both form and function at all three stations.

The evolutionary picture which the genus *Zauschneria* presents is a fascinating one. Although nothing is known of their origin, there are three diploid species in very different and remote environments, each fitted to its surroundings by genic differentiation alone. While each of the three appears to be in good genic equilibrium, they differ by many genes, which, when exchanged across the specific barriers in all proportions in the F_2 , disturb the metabolic rate in the resulting offspring. This renders these offspring incapable of survival.

Two ecologically very different autotetraploids may have arisen from two or even all three of the diploids, creating two ecotypes of a new tetraploid species; they were both separated from the diploids by chromosomal barriers. Finally, by hybridization, the two new tetraploid ecotypes might have crossed to form a third which was capable of occupying the territory left between them. This new tetraploid species, now with three major ecotypes, is still able to absorb genes from the diploids, and has probably been doing so continually, increasing the variation and the complexity, and giving rise to the present complex, the cenospecies *Z. californica*.

Zauschneria is an excellent example of the evolution of the heteroploid complex, a term proposed by Babcock and Stebbins (1938).

It belongs with the sexually propagating complexes, and the barriers separating its four ecospecies are still very definite, as the crossings indicate. It also suggests how a genus might become rejuvenated and "aggressive" through polyploidy, how auto- and allopolyploids may merge into one another, how the barriers between genetically separated diploid species break down when polyploids arise from them, and how species may have a polyphyletic origin.

VII

PENSTEMON: A STUDY IN CYTOTAXONOMY AND TRANSPLANTING

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Penstemon, a member of the Scrophulariaceae, is principally confined to temperate North America, although it is not rare as far south as southern Mexico and as far north as Alaska. It contains some three hundred recognized species, all but one of which are confined to this continent; the exception occurs on the northeastern Asiatic islands. Members of the genus occupy almost all available sorts of habitats from desert floors to high alpine peaks, and attain their greatest differentiation in western North America. In this respect there is an analogy with the species of *Potentilla* treated in earlier chapters, but as to the general method of differentiation the situation is new.

Some of the first transplants used by Dr. Hall were *Penstemons*, and many additions have been made since. These plants are not as satisfactory subjects for varied-environment experiments as the *Potentillas*, for they require more delicate handling; but the extensive taxonomic problems in *Penstemon* have long engaged the attention of one of the authors, Keck, and many general data have been gathered on its members. Representatives of almost all the principal groups, including scores of species, have entered the transplant experiments from time to time, but data in the present report will be drawn principally from three groups: the *Proceri*, section *Erianthera*, and the *Glabri*.

Our transplant experiments have dealt with groups that have not undergone complete taxonomic revision as yet. In the present report only such taxonomic accounts and descriptions are given as are needed to document the experimental findings; changes in nomenclature are made only in those cases in which the procedure seems to be obviously justified. Suspected improvements elsewhere will await further studies on the various groups.

A survey of the chromosome situation in approximately fifty species of *Penstemon* shows that, barring a single exception, all follow an 8 series, and that the great majority of the species are diploid, with $n=8$. The lone exception is *Penstemon nemorosus* (Dougl.) Trautv., in which $n=15$. This plant, interestingly enough, has been more often treated by writers of floras as a *Chelone* than as a *Penstemon*; but its closest relative is undoubtedly *Penstemon Lyallii* A. Gray, a species whose chromosome number, unfortunately, has not been determined. These two species have much in common with members of the section *Erianthera*, but Pennell and Keck propose to erect a section *Nothochelone*, embracing *P. nemorosus* and *P. Lyallii*. Certainly the outstanding chromosome number of *P. nemorosus*, in a genus that is otherwise so consistent, points to sectional status for that species.

DIFFERENTIATION IN THE PROCERI

This subsection within the subgenus *Eupenstemon* presents a story of cyto-ecological differentiation. Many species are involved. All follow an 8 series in chromosome number, with relatively few polyploids. This group is widely spread throughout the western United States, and its members are set off at times by differences in chromosome number, and at times by genic differentiation only.

The picture that they present, based upon structural, distributional, and cytological similarities and differences, is suggestive of the general situation in the group and offers a new viewpoint on the relationships within the subsection. The results are not yet complete enough to clarify the entire picture of this group, for four reasons: (1) not all the members of the subsection have been available for this investigation; (2) the cytological findings have sometimes been difficult to correlate with taxonomic key characters; (3) perhaps hundreds of additional chromosome counts need to be made in order to define more precisely the cytological boundaries between the units; and (4) nothing is known of the genetic relationships between the units, for crossing experiments have not been attempted.

In the *Proceri* there appear to be several evolutionary trends. At all events it seems quite certain that the members of this group do not represent different steps in the development of only one line. By using one of the most obvious distinctions that seem to have phyletic significance, the subsection can be divided into those spe-

cies with entire leaves and those with toothed leaves. In the latter subdivision are some species whose members are prevalently entire-leaved, but which, through the occasional development of teeth and other characteristics, indicate their common ancestry with other members of this group.

THE ENTIRE-LEAVED PROCERI. In figure 104 important members of the entire-leaved group of *Proceri* are shown. On the whole, fundamental structural features of the flower and fruit are much the same throughout all the species of the *Proceri*, and speciation has been marked by differences in life form, vegetative parts, size, vesture, and so on. Such differences are of the sort that might mark either ecotypes or ecospecies and ordinarily require cytogenetic corroboration for their true evaluation. Almost all the members of the entire-leaved group of *Proceri* are true hemicryptophytes and form almost no wood.

Penstemon procerus Dougl. ex Grah. is a very widespread species that offers many problems. It is illustrated by the lower row of plants in figure 104. The two specimens on the left represent at least different ecotypes from mid-altitude and alpine conditions in the Sierra Nevada; the central specimen, from the Great Basin, is from the eastern base of the Sierra Nevada; the fourth came from the Wasatch Mountains of Utah; and the right-hand specimen came from the Rocky Mountains of Colorado. The first four of these widely separated plants are diploid ($n=8$), but the Rocky Mountain plant is tetraploid ($n=16$).

Only minor morphological differences have been detected between the materials of *Penstemon procerus* represented by the Utah and Colorado specimens, so that systematists have been able to separate one only as a variety from the other. The Colorado plant is considered true *P. procerus* Dougl. ex Grah., while the Utah plant is var. *aberrans* (Jones) A. Nels. No taxonomist working on the Rocky Mountain flora has ever suggested that these belonged in different species. Nevertheless, genetically they do. Lacking sufficient data from that region, we are unable to say where the change in chromosome number takes place. Also, we are equally uncertain whether material from the type locality of *P. procerus*, which is either in Saskatchewan or in Alberta, where Drummond collected the original seed well over a century ago, is diploid or tetraploid.



FIG. 104. Representative entire-leaved *Proceri* and their chromosome numbers.

Above: left, *Penstemon cinicola* from volcanic sand, north of Lapine, Deschutes County, Oregon, at 1285 m.; center, *P. attenuatus* from the Blue Mountains in Umatilla County, Oregon, at 1160 m.; right, *P. confertus* from Meacham, Umatilla County, Oregon, at 1100 m.

Below: forms of *P. procerus*, from left to right: a mid-Sierran race from Aspen Valley, Yosemite Park, California, at 2010 m.; an alpine race (*heterodoxus*) from Tioga Pass, Tuolumne County, California, at 3030 m.; a Great Basin form from near Mono Lake, Mono County, California, at 2070 m.; var. *aberrans* (Jones) A. Nels. from the Tushar Range of the Wasatch Mountain system, west of Puffer Lake, Beaver County, Utah, at 2750 m.; and a tetraploid from the Rocky Mountains at Camp, North Park, Jackson County, Colorado, at 2600 m.

The specimens were all collected in the field, except *P. confertus*, which was taken as a transplant voucher in a garden at Mather.

In the Sierra Nevada of California there is considerable variation, but some forms are scarcely separable from *P. procerus* of Utah and Colorado. It seems a reasonable assumption that the diploid members of this assemblage will all prove to belong to one ecospecies, within which several ecotypes have been differentiated that are recognizable as subspecies. In fact, the California material has long gone under the name of *procerus*.

There are significant differences between the three California forms of *procerus* shown in figure 104. The mid-Sierran specimen is a tall meadow form from the lower limits of the Canadian life zone. It occurs in grassy swales surrounded by a forest of *Abies concolor* and *Populus tremuloides*.

The little alpine specimen next to it grows in alpine meadows near tree line. It differs from all the other plants illustrated in figure 104, in that its flowers are usually reduced to one verticil, and its inflorescence is glandular-pubescent. All the others are glabrous throughout. The glandular character seems to mark specific lines in other parts of the *Proceri* and may be of equal importance here, for the glabrous type also is found in a dwarf form above tree line in the central Sierra Nevada, where both the glandular and the glabrous type exist in fairly unmixed isolated populations. However, the glandular-pubescent type of our illustration is the abundant form in the alpine zone. It has been named *P. heterodoxus* Gray.

The tall plant from the Great Basin grows in the sod of damp meadows. While fundamentally similar to the mid-Sierran plant, it seems very different from either of the preceding because of its much coarser and somewhat glaucous stems and herbage. These characteristics would be expected in a plant that grows in the Great Basin, where sagebrush (*Artemisia tridentata*) is the dominant land cover.

The cytological constancy of these three very different types is the more remarkable when we consider that the diploid from Utah and the tetraploid from Colorado are morphologically scarcely distinguishable!

Penstemon Tolmiei Hook., not illustrated, is another diploid dwarf alpine form of *P. procerus*, parallel to *heterodoxus* but glabrous throughout. It occurs farther north in the Cascades of Washington and northern Oregon and is found at and above tree line.

In summary, we would include in *Penstemon procerus* plants that are found from western Manitoba to British Columbia and south-

ward through the mountains to central Colorado and Utah, Washington, Oregon, and the southern Sierra Nevada of California.

Two other tetraploid species are shown in figure 104, as well as a hexaploid species.

Penstemon cinicola Keck is a newly recognized species (described on p. 294). It occurs only on volcanic ash in that great region of lava flows east of the Cascade Mountains in central Oregon and probably south to the lava beds of northern California. Its precise boundaries must be worked out with the aid of cytology, for certain outstanding characters, such as the diminutive calyx, which were thought to mark this unit clearly have been discovered in diploid forms of *P. procerus* from the borders of this region. Also, the peculiar habit of the plant, in failing to develop a basal rosette as do the meadow-dwelling members of *P. procerus*, must be verified a number of times by chromosome counts before it can be accepted as correlated with the tetraploid chromosome number. We have counted chromosomes in plants (thereby verified as *procerus*) from meadows in the same local region in which *P. cinicola* is found growing on ash. Hybrids between the two have not been discovered.

Penstemon confertus Dougl. ex Lindl., shown in figures 104 and 112, is constantly different from the blue-purple-flowered *P. procerus* in having yellow flowers. In other characters the two species are scarcely separable. It is a well-defined tetraploid unit of grassy slopes and open woodlands of central Idaho and eastern Washington and Oregon. Several populations of *P. procerus* from this general region which have been examined cytologically are diploid, so the two species appear to have a chromosomal barrier between them.

The hexaploid species shown at the top of figure 104 is *P. attenuatus* Dougl. ex Lindl. It is found within the same general area as *P. confertus*, i.e., in central Idaho and eastern Washington and Oregon. It usually has blue-purple flowers, but particularly in north central Idaho it is frequently yellow- or whitish-flowered. Colonies of either blue- or yellow-flowered plants may appear close together in the same sort of environment—habitats similar to those of *P. confertus* and *P. procerus*. Furthermore, while it is usually found with entire leaves, it may rather frequently develop fine teeth, suggesting the influence of one or another of the toothed-leaved species mentioned below. It has a glandular-pubescent inflorescence, which is of exceptional occurrence among the entire-leaved members of the *Proceri*,

but is the usual condition among the toothed-leaved species. *Penstemon attenuatus* is larger-flowered and more robust than either *procerus* or *confertus*, characters which are in keeping with its higher chromosome number.

There is another entire-leaved hexaploid, the cytological counterpart of *attenuatus*, that should be mentioned, which is not illustrated. This is *P. euglaucus* English, an endemic of the Cascade Mountains of Washington and northern Oregon. It has glaucous, ample, rather thick foliage and blue-purple flowers considerably larger than those of *procerus* and *confertus*.

Three other entities should be mentioned before we turn our attention from the entire-leaved species. There is an especially beautiful *Penstemon* in the mountain meadows of northeastern Oregon and west central Idaho. In habit it is similar to the meadow-dwelling *procerus*, and it has entire leaves, glabrous herbage, very broad, scarious sepals, and large, deep blue flowers aggregated into a terminal globose cluster, whence the specific name, *P. globosus* (Piper) Pennell & Keck. This species is shown in figure 112. It is tetraploid, $n=16$.

Another tetraploid that is apparently a very close relative of *P. globosus* occurs to the eastward, from south central Idaho to southern Wyoming, northwestern Colorado, and the mountains of Utah. This is *P. aggregatus* Pennell, and it differs from *globosus* in having a naked instead of a leafy inflorescence, lanceolate instead of ovate leaves, smaller sepals, and somewhat smaller flowers. It likewise grows in high montane to alpine meadows and is a considerably taller plant than *procerus*.

A white-flowered form from Elko County, Nevada, that grows in moist spots similar to those inhabited by the Great Basin form of *procerus* in the sagebrush association, is *P. pratensis* Greene. The precise relationships of this form have not been worked out. The flower color and chromosome number ($n=16$) are suggestive of a connection with the yellow-flowered *P. confertus*, which is otherwise a long distance to the north. On general morphology this coincides quite as well with forms of *procerus*, which, of course, has also been shown to have a tetraploid form.

THE TOOTHED-LEAVED PROCERI. Representative members of the toothed-leaved subdivision of the *Proceri* are shown in figure 105. In contrast with the situation in the preceding species, in which

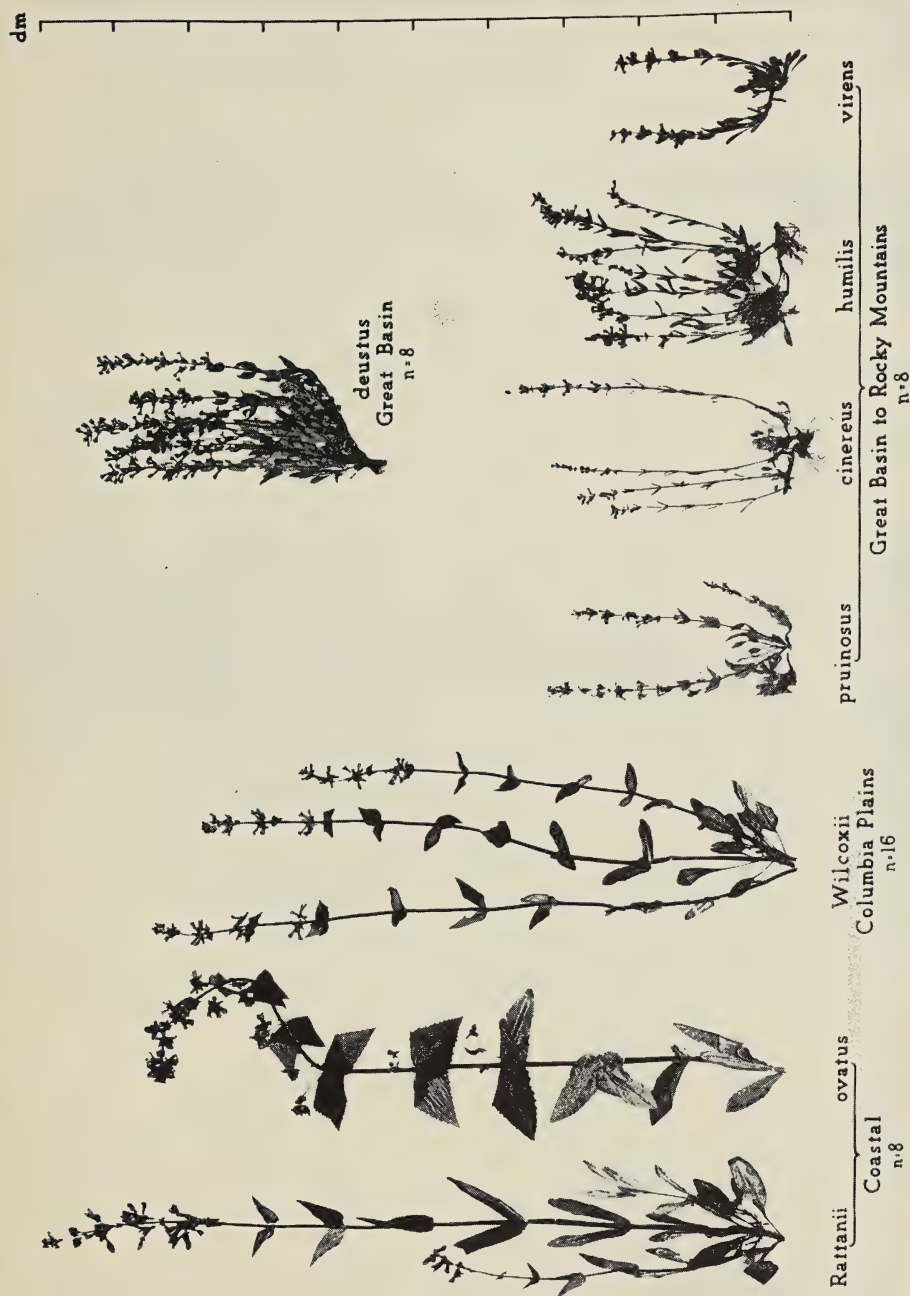


FIG. 105. Representative toothed-leaved *Proceri* and their chromosome numbers.

Left to right: *Penstemon Rattanii* ssp. *Kleei* from Mount Madonna, Santa Clara County, California, at 425 m.; *P. ovatus* from Cape Horn, Skamania County, Washington, at 20 m. (a Stanford-grown seedling); *P. Wilcoxii* from near Bingen, Klickitat County, Washington, at 150 m. (a transplant at Mather); *P. pruinosis* from near Lind, Adams County, Washington, at 400 m.; *P. cinereus* from Bend, Deschutes County, Oregon, at 1100 m.; *P. humilis* from near Dixie Mountain, Grant County, Oregon, at 1280 m.; *P. virens* from south of Colorado Springs, El Paso County, Colorado, at 1850 m.; and (above) *P. deustus* from near Pocatello, Bannock County, Idaho, at 1400 m.

most were glabrous throughout and relatively few were glandular, all the members of this group are glandular-pubescent within the inflorescence.

On the left in figure 105 are two very robust species of the Coast Ranges in which one might expect (after examining the situation in the entire-leaved species) a rather high chromosome number, but these are diploids, $n=8$. On the left is *P. Rattanii* Gray, which grows at relatively low elevations along the coastal hills from Coos County, Oregon, to Humboldt County, California. Both ssp. *typicus* and ssp. *Kleei* (Greene) Keck, the form illustrated, which has smaller sepals and is now isolated in the Santa Cruz Mountains some 260 miles to the south of *typicus*, have been examined and found to be diploid. An interior, high-montane form, originally held in varietal rank under *Rattanii*, but probably a distinct ecospecies (a complete series of intergrades between this small-flowered, slender plant and the large-flowered, robust *Rattanii* has not been found) is *P. minor* (Gray) Keck, and it is also diploid.

Next to *P. Rattanii* in the figure is *P. ovatus* Dougl., from the Columbia River. This species is rather local around the Columbia Gap in both Washington and Oregon, but a form in north central Idaho appears to be morphologically indistinguishable. This has not been thoroughly investigated, but it may well prove to be the same, for other examples are well known of coastal species reappearing in this portion of Idaho. Winge (1925) previously determined that this species is diploid.

The third plant from the left in figure 105 is a tetraploid species, *P. Wilcoxii* Rydb. We would include here all the toothed-leaved tetraploids from western Montana to central Washington. These are large-leaved, coarse herbs with blue-purple flowers, and form a fairly homogeneous unit. Much of this material has been classified previously as *P. pinetorum* Piper.

To the lower right in figure 105 appear four members of a diploid group that form a considerable complex. Probably several ecotypes are morphologically distinguishable in it. *Penstemon pruinosus* Dougl. ap. Lindl. is found from the east flank of the Cascades in Washington to Idaho, western Montana, and adjacent Canada. Its leaves are more prominently toothed than those in the following species. Probably *P. albertinus* Greene, which is also diploid, belongs to this species.

Penstemon cinereus Piper occurs in volcanic ash in the upper Deschutes Valley of central Oregon, and southward to Siskiyou County, California. Comparison of the photograph of this plant with that of *P. cinicola* in figure 104 brings out many dissimilarities, yet these species occupy the same specialized ecological niche. *Penstemon cinereus* is probably a far western development of the widespread *P. humilis* Nutt., which is found across southern Idaho to western Wyoming, and from northern Nevada to northwestern Colorado. A key difference is in the shape and vesture of the basal leaves. The specimen shown in our illustration of *P. humilis* is somewhat atypical, because it came from eastern Oregon, at the far western extension of the range of the species, and very possibly represents a distinct subspecies. It clearly shows the development of a woody base, a frequent but not universal feature of *humilis*. In other words, this species is sometimes, at least, a true chamaephyte.

The specimen on the extreme right in figure 105 is *Penstemon virens* Pennell, the Rocky Mountain counterpart of *P. humilis*, occurring at moderately high elevations from southeastern Wyoming to southeastern Colorado. It is distinguished in particular by the larger flowers and greener herbage.

In this same figure we have also placed *P. deustus* Dougl. ex Lindl., a decidedly toothed-leaved chamaephyte with small, whitish flowers that are marked within with purple guide lines. This species finds its closest affinities in the *Proceri*, but it seems to stand somewhat to the side of the others; from a number of minor distinctions it is less obviously related to any of the other species than they are to each other. It is widespread in semiarid habitats from northern Wyoming to central Washington and southward to central Nevada and California. It also is diploid, $n=8$. This confirms Heitz' (1927) observation.

PROBABLE RELATIONSHIPS OF THE PROCERI. We have attempted in figure 106 to sketch the probable situation in this complex as far as it is reasonably well known from the present data. In this figure are shown very diagrammatically the various units mentioned in the preceding discussion in their relative geographical and supposed phyletic positions. *Penstemon ovatus* and *P. Rattanii* are on the left, suggestive of their position on the West Coast. They are surrounded by a common line, indicative of a degree of relationship, but the con-

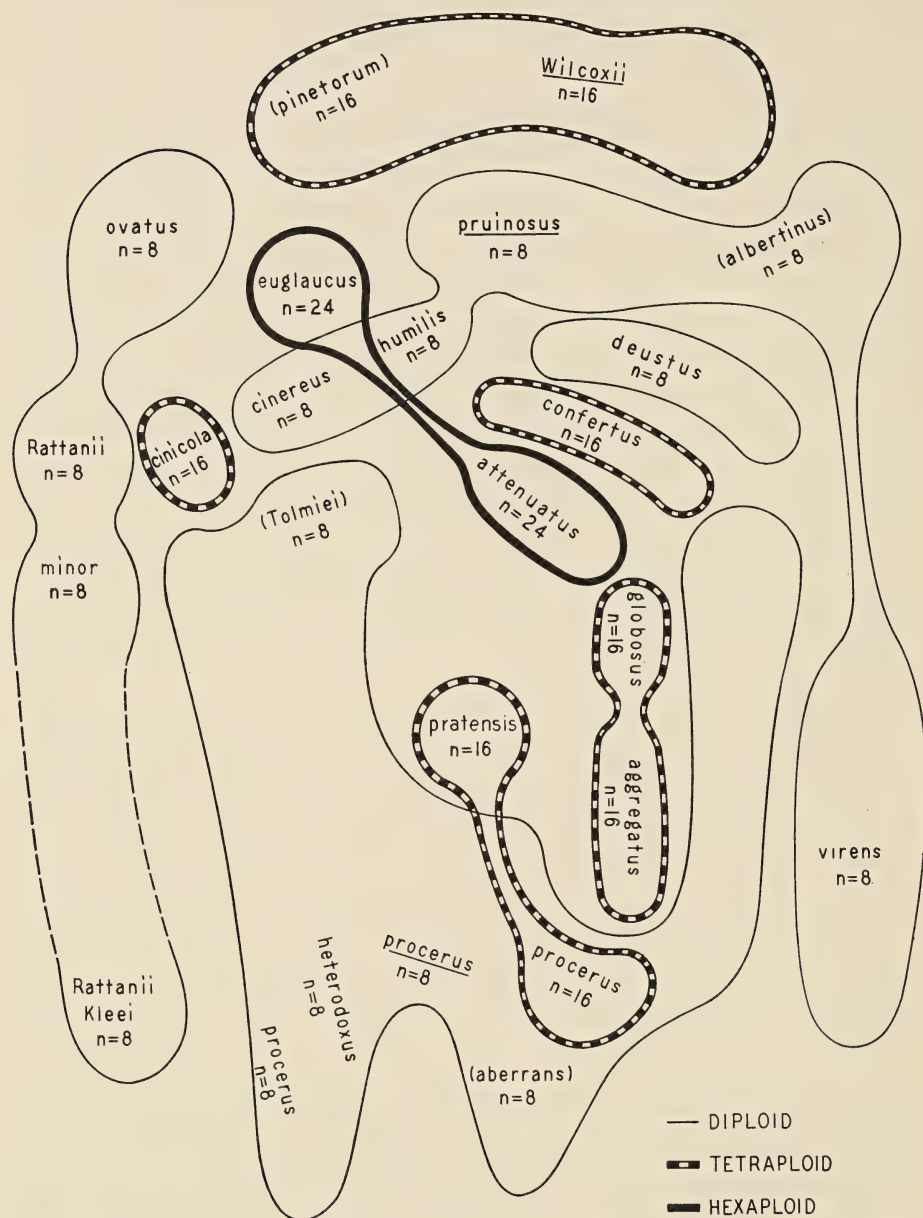


FIG. 106. Diagram showing relative geographical distribution, chromosome numbers, and probable degrees of relationship of various species of the *Proceri* Penstemons. See text.

striction between them indicates that this is not very intimate. *Penstemon Rattanii* is shown in the central part of the coastal area and its ssp. *Kleei*, which is separated from it in nature by a true hiatus of more than 250 miles, whence the broken line, is at the southern end of the figure. The chromosome situation is also depicted. For the sake of clarity it has seemed advisable to make the geographical boundaries no more than suggestive; the actual boundaries may be found more accurately in the preceding text.

This diagram may serve a useful purpose in depicting our present concept, so that when data become available from other important members of the *Proceri*, such as *Penstemon Watsonii* Gray, *P. radicosus* A. Nels., *P. aridus* Rydb., *P. Rydbergii* A. Nels., *P. pseudoprocerus* Rydb., *P. oliganthus* Woot. & Standl., and *P. gracilis* Nutt., they can be added.

Penstemon procerus is shown as an inclusive figure within which there are several forms that may be ecotypes. The tetraploid form of *procerus*, included within the figure, is shown attached to the tetraploid *pratensis*, which is excluded from the figure, expressing the doubtful status of the latter at this time.

Judging from the morphology, *P. cinicola* and *P. aggregatus* could have arisen from very different races of *procerus* by autopolyploidy. Some features of *cinicola*, such as the diminutive truncate calyx, the exceptionally small flowers, and the characteristic leaves, are found also in the diploid *procerus* of the same region but not at random through the species. The chromosome situation is not conclusive as to the origin of the polyploids.

Most of the polyploid *Penstemons* that we have examined are rather irregular cytologically, with some degree of multivalent association. In the *Proceri* this is the case with the tetraploids (and especially with the hexaploids), except that *Wilcoxii* is more regular than the others. In *cinicola* this condition might indicate either autotetraploidy, or that it has been produced by allopolyploidy from diploid species whose chromosomes were highly homologous. A similar uncertainty exists as to the origin of the tetraploid, yellow-flowered *confertus* and of *globosus*.

It seems likewise possible that the hexaploid *attenuatus*, which has both yellow-flowered and blue-flowered races, may have originated through a combination of the glabrous *confertus* and either *pruinosis* or *humilis*, which are blue-flowered diploids having glandular-pubes-

cent inflorescences and slightly serrate or entire leaves. Perhaps the most likely way of reproducing the hexaploid *euglaucus* from present-day species would be to combine the tetraploid *globosus* and diploid *procerus* forms. At present *globosus* is found no nearer to the home of *euglaucus* in the Cascades than the Wallowa Mountains, in the northeastern corner of Oregon, but this situation may have been very different in the past.

We have placed the western arm of *P. Wilcoxii* (the *pinetorum* form) approximate to both *P. ovatus* and *P. pruinosus*, because this is where it geographically occurs. Its morphological characters, which are intermediate between these two diploid species, and its chromosome number suggest amphidiploid origin similar to that of *P. neotericus* of the section *Saccanthera* (Keck, 1932; Clausen, 1933).

SUMMARY. In closing this account of cytotaxonomic problems in the *Proceri*, we are impressed with the great diversity that is congregated in the Columbia River basin. Diploids, tetraploids, and hexaploids are all present, and there are members of the group available to occupy almost every one of the different environmental zones in the mountains of that region. The number of unlike forms decreases as one travels away from that center, and the cytological diversity becomes less. Genic differentiation, in connection with differences in chromosome number and ecologic differentiation, has apparently played a leading rôle in speciation in this group.

TRANSPLANT INVESTIGATIONS IN THE PROCERI

Several distinct altitudinal races of *Penstemon procerus* are found in the central Sierra Nevada of California. At the three transplant stations these exhibit very different reaction patterns in many respects, including vigor and earliness, indicating that they belong in different ecotypes. Four representatives of these ecotypes are shown in figure 107. The specimens in the left-hand row were taken at the time the plants were dug. The difference in morphology is remarkable because all these ecotypes are found in cool, moist, meadowy places, are very frost-resistant, and may be considered as plants characteristic of high elevations.

Those that descend the lowest in the Sierras (see 1243-4, from Miguel Meadows, fig. 107) are found in meadows where they receive some protection from the sun in the heat of the day. Also, very few

colonies are found in this general region below 2000 m. This fact is of interest in connection with the transplant evidence, which shows that these plants as a whole thrive best at Timberline, only moderately well at Mather, and definitely poorest at Stanford. At Mather their vigor is considerably reduced by the dry conditions and high day temperatures. At this station they grow best in the moist sun garden—a result that might be expected, for in their natural habitats their shallow roots are always found in moist soil.

Since all these races react very much like subalpine or alpine ecotypes, their appreciable morphological diversity, which is correlated with the altitudes of their natural habitats, is impressive. On first sight the situation would seem to parallel that in *Horkelia fusca* (p. 207), in which the altitudinal diversity in the central Sierras is comparable with this, and in which no true mid-altitude ecotype is developed. But in *Penstemon procerus* the taller members of the series from lower elevations differ very much in earliness, for the Miguel Meadows race is one month or more later than the Aspen Valley race at all stations; this can be seen from figure 110. The races of *Penstemon procerus*, therefore, parallel the reactions of the ecotypes of *Potentilla glandulosa*, for the meadow ecotype of the latter species, ssp. *Hansenii*, is very tall and very late, the subalpine ecotype, ssp. *nevadensis*, is tall and fairly early, and the alpine *nevadensis* is small and very early.

MODIFICATION. The gross morphological modifications that appear at the three transplant stations are shown in figure 107. The decline in all races at Stanford is evident, even though the specimens in the figure are the best we have in our collections. The plant of the Tuolumne Meadows race (1247-2), from a subalpine altitude, is represented as producing only a rosette at Stanford. Examination of the survival chart (fig. 111), however, shows that another clone from the same locality managed to flower three consecutive years at Stanford, while other races of the species, from other localities, often fail to flower there.

The poor success of the Miguel Meadows clone (1243-4) at Timberline is striking. Proportionately, it shows the greatest decrease in stature of any race. As is shown in the survival chart (fig. 111), it flowers in nearly all years, but very rarely ripens seed there. The other three races, however, from Aspen Valley to Tioga Pass, a vertical range of 1000 m. in elevation, grow more vigorously at Timberline

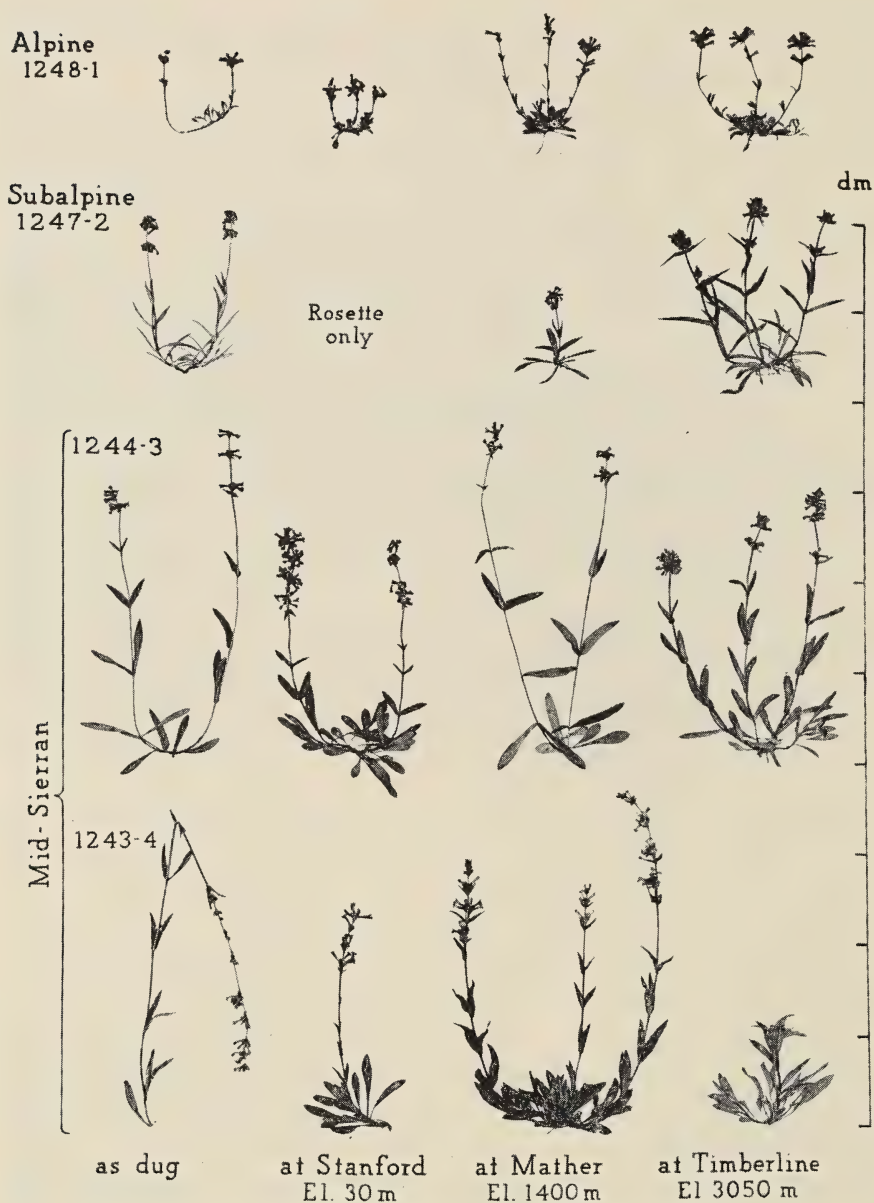


FIG. 107

(Legend on opposite page)

than at the other stations. Also, they ordinarily ripen annually at least some fruit there, the alpine ecotype attaining full maturity without exception.

The increased vigor at Timberline is even more evident from an examination of the graph in which number of stems is tabulated (fig. 108). The relatively poor success shared by all races at Stanford and Mather is reflected by the low average number of stems of each at both of these stations; but all races show a marked upturn in the number of stems produced at Timberline. Even the Miguel Meadows race shares in this increase. Such vigor at Timberline is usually found only in plants from high altitude.

One of the most interesting modifications in this species is the reduced number of verticils or "whorls" in the inflorescences of the plants grown at Timberline. This character has received considerable taxonomic attention, for it has been made the basis of a species, *P. geniculatus* Greene, an alpine form in which the flowers are reduced to one verticil. Our experiments show, however, that the number of verticils depends to a considerable extent upon environment, as is shown in figure 107. Conditions far removed from the native habitat often cause the verticils to become very much crowded together and simulate a single one. This indicates that unfavorable conditions may be a determining factor. Since the limits of modifiability for this character prove to be broad, its employment as a principal mark distinguishing species is subject to criticism.

The very different behavior of the Miguel Meadows race, from 1650 m. elevation, and the Aspen Valley race, from 2010 m., was unpredictable, especially since they are morphologically scarcely dis-

FIG. 107. Modifications in clones representing altitudinal races of *Penstemon procerus* from Yosemite Park grown at three stations. All are diploid, $n=8$.

Top row: 1248-1, dug September 13, 1926, at Tioga Pass, at 3030 m.; set at Stanford in 1929 (from a division held at Berkeley), at Mather in 1934, and at Timberline in 1930. The Stanford specimen was taken in 1935, the others in 1936.

Second row: 1247-2, dug September 14, 1926, at Tuolumne Meadows, at 2740 m.; set at Stanford in 1934 (where it remained in a non-flowering state in the following years), at Mather in 1927, and at Timberline in 1934. The Mather specimen was taken in 1932, the Timberline one in 1936.

Third row: 1244-3, dug July 10, 1927, above Aspen Valley, at 2010 m.; set at Stanford in 1934, at Mather in 1928, and at Timberline in 1930. Specimens taken in 1935 except at Mather in 1931.

Bottom row: 1243-4, dug July 21, 1927, from Miguel Meadows, at 1650 m.; set at Stanford in 1934, at Mather in 1928, and at Timberline in 1930. Specimens taken in 1936 except at Timberline in 1935.

tinguishable, and since very few colonies of the species are known in this region from below 2000 m.—a fact that would lead one to

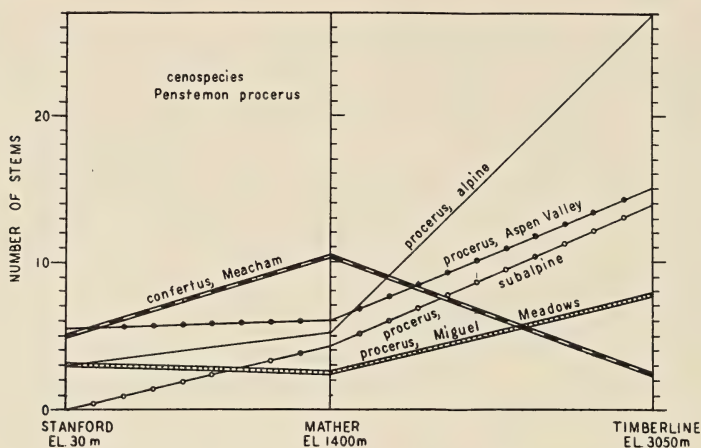


FIG. 108. Modifications in number of stems in clones representing altitudinal races of the *Proceri* *Penstemon*s grown at three altitudes.

Data averaged from the years between 1928 and 1937. The graphs represent one individual each of *confertus*, Meacham, and *procerus*, Miguel Meadows, and two individuals of each of the other races.

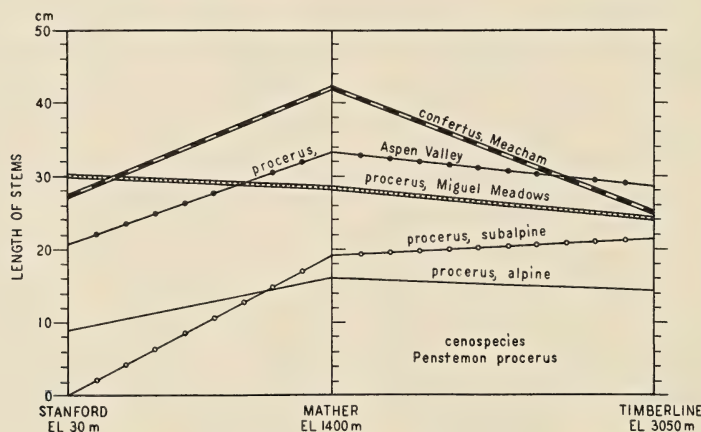


FIG. 109. Modifications in length of stems in clones representing altitudinal races of the *Proceri* *Penstemon*s grown at three altitudes. Data from the same sources as in figure 108.

suspect that the Miguel Meadows race was a pioneer from higher elevations. Rather, the morphological gap is between the Aspen Valley and the Tuolumne Meadows races, which are separated by 730 m.

vertical elevation, but still these races react like members of one ecotype.

Racial differences in lengths of stems are shown graphically in figure 109. The data are based on only eight plants but are averaged from a series of years between 1928 and 1937, inclusive. They are less complete for Stanford, because none of the *Proceri* did very well there, although, of all the Penstemons, they were the ones that prospered most at the three stations. There is a slight tendency for plants from mid-altitude to grow tallest at Mather and for those from high altitude not to increase in height there. But length of stem varies considerably in the populations. For example, not nearly all subalpine plants are as dwarf at Mather as 1247-2 of figure 107. This is evident from the tabulations below, giving height and earliness of the eight plants at Mather, averaged from the period of years mentioned above. This tabulation also shows that there is no significant difference in height between the plants from subalpine conditions and those from mid-altitude.

PLANT NUMBER AND ORIGIN	AT MATHER	
	Longest stem (cm.)	Date of first flowers
Mid-altitude:		
1243-4, Miguel Meadows, 1650 m.....	28.2	June 24.5
1244-3, Aspen Valley, 2010 m.....	42	May 24
-4, Same.....	24.8	May 24.0
Subalpine:		
1246-1, Mineral King, 2390 m.....	27.0	May 28.7
705-D, Tuolumne Meadows, 2740 m.....	24.3	May 20.0
1247-2, Same.....	6.5	May 24.0
Alpine:		
1248-1, Tioga Pass, 3050 m.....	14.5	May 18.7
-2, Same.....	17.7	May 16.3

There are great differences in earliness between plants from low and high elevations. At Mather there is a difference of five weeks between the appearance of the first flowers of the Miguel Meadows plant from 1650 m. and of the Tioga Pass plants from 3050 m. altitude. This is based on averages of five years. The plants from Aspen Valley and the subalpines from Mineral King and Tuolumne Meadows are approximately one week later than the alpiners. At Timberline a similar difference is maintained according to a three- to seven-year record. The two alpiners are the earliest, the subalpines

and the Aspen Valley plants are twelve to fourteen days later, and the Miguel Meadows plant is about five weeks later still, as shown in the graph, figure 110. At Stanford the differences in earliness are

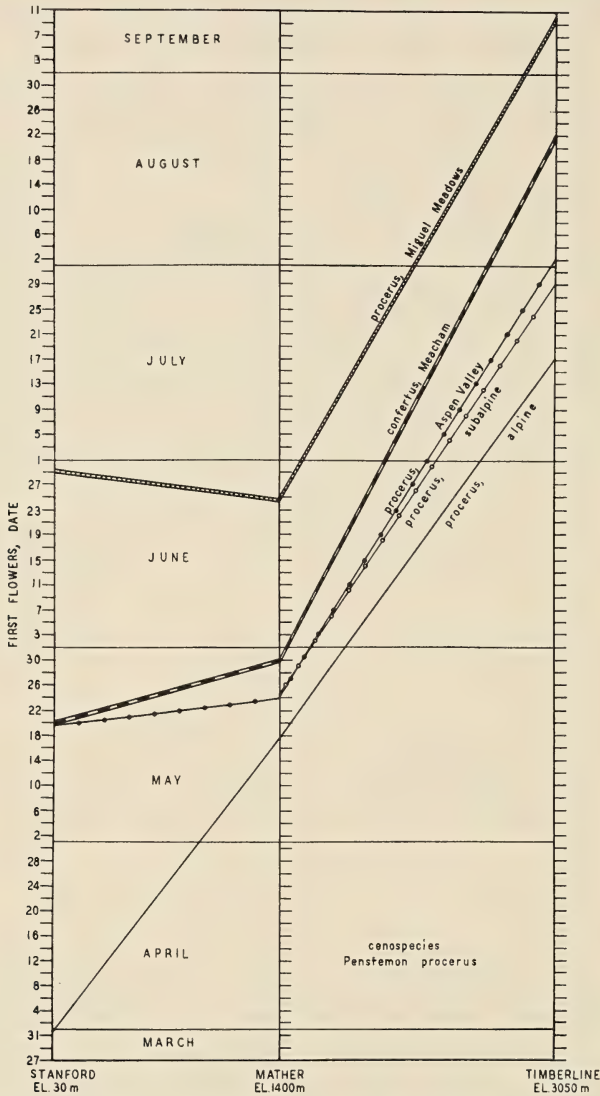


FIG. 110. Modifications in earliness in clones representing altitudinal races of the *Proceri* *Penstemons* grown at three altitudes. Data from the same sources as in figure 108.

even more spectacular, but the record is less dependable, because here these plants usually produce rosettes only, and flower erratically.

Penstemon procerus survives very well at Timberline, as shown by

the survival chart, figure 111. The forms from Aspen Valley and from higher altitudes are all early enough so that they have ample time for maturing of seed at Timberline every year. The Miguel Meadows plant, however, flowers too late to be able to mature seed except in years with a very early season. At Mather, all forms flower, mature seed, and survive rather well. The general impression of fair success at all three stations indicated by figure 111 needs to be modified by the statement that many more plants have been tried and lost before results even as complete as these were obtained.

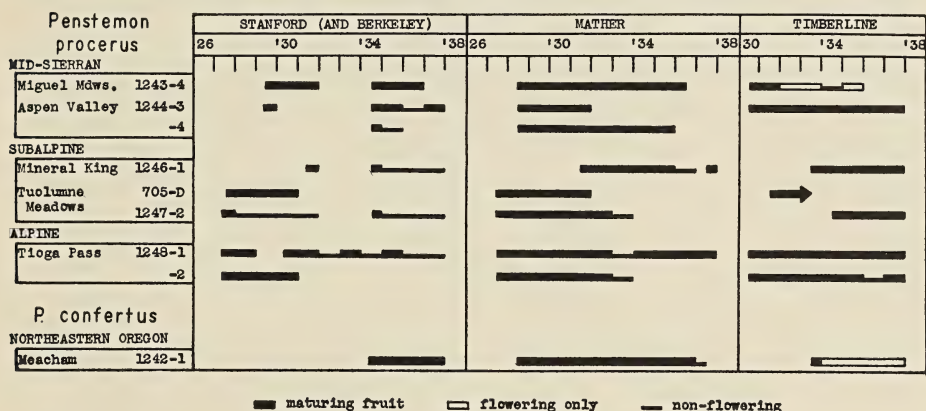


FIG. 111. Record of survival and flowering of clones representing altitudinal races of the *Proceri* Penstemons. See text for fuller explanation.

Too few plants survived in the experiments to warrant definite conclusions regarding the number of ecotypes of *Penstemon procerus* that exist in the central Sierra Nevada. Plants from the highest elevations are dwarf and early under all conditions. Combining this information with observations in the field, it appears that there is an alpine ecotype near tree line. Roughly between 2000 and 2800 m. elevation there is a later and taller form, which from its reactions may be classified as a subalpine ecotype, because it survives and matures at Timberline. It seems to pioneer downward and includes the Aspen Valley plants. Finally, the form from Miguel Meadows probably represents a mid-altitude ecotype that survives but does not mature at Timberline. The information gained from experiment, that *Penstemon procerus* flowers poorly at Stanford and produces large numbers of stems at Timberline, corroborates the impression gained from field studies that this species is basically alpine in

nature. It has developed ecotypes to fit other environments, but these are not very adaptable to lower elevations, as is indicated by the many plants that died before they could be distributed to all three stations.

OTHER SPECIES OF PROCERI. *Penstemon confertus* has been grown for eleven years from a series of five plants dug at Meacham, in the Blue Mountains of northeastern Oregon, at 1065 m. elevation. The reactions of these plants are shown in the graphs with *P. procerus* (figs. 108 to 111). The general appearance of a clone of this species at the three stations is shown in figure 112. The most striking difference between the Meacham plant of *confertus* and the preceding races of *P. procerus* is that whereas the latter behave like subalpine and alpine ecotypes, the former is definitely a mid-altitude ecotype in its reactions. It grows obviously better at Mather than at the other two stations, which is to be expected since the conditions at this station most closely parallel those of its native habitat. This tetraploid species is considerably more vigorous there than any of the forms of the diploid *procerus*, as shown by its greater height and increased number of stems. But it also grows somewhat taller and produces more flowering stems at Stanford than at Timberline, an opposite reaction from that of any of the races of *procerus*. It flowers considerably later at all stations than the Sierran forms of *procerus* except the Miguel Meadows race, and is never able to ripen seed at Timberline. It is very frost-resistant, however, and survives well at the alpine station.

Penstemon globosus has been represented in the cultures for eleven years by ten plants of two races from the Wallowa Mountains of northeastern Oregon. One, 1238, is from Lake Basin, at 2440 m. elevation, and the other, 1239, is from the Wallowa River above Wallowa Lake, at 1675 m. elevation. While the latter culture was taller at Mather than the former, there were insufficient data to measure the significance of this observation, and there was no appreciable difference in earliness between the cultures. The modifications of an individual from one of these, 1239-4, are shown across the upper row in figure 112. Like the forms of *procerus*, these races are better suited to alpine environments than to lower altitudes. At Stanford this species usually grows as a weak rosette only and flowers very exceptionally. At Mather it grows fairly satisfactorily, but better in

globosus $n=16$

1239-4

**confertus** $n=16$

1242-1

at Stanford
El. 30 mat Mather
El. 1400 mat Timberline
El. 3050 m

FIG. 112. Modifications at three altitudes in clones of *Penstemon globosus* and *P. confertus*. Both are tetraploid, $n=16$.

Above: 1239-4, dug September 5, 1927, above Wallowa Lake, Wallowa County, Oregon, at 1675 m.; the propagules were planted at Stanford in 1929, at Mather in 1928, and at Timberline in 1933; the specimens were taken at Stanford in 1932, and at the other stations in 1935.

Below: 1242-1, dug September 1, 1927, near Meacham, Umatilla County, Oregon, at 1100 m.; the propagules were planted at Stanford in 1934, at Mather in 1928, and at Timberline in 1933; the specimens were taken at all three stations in 1935.

the moist sun than in the interstation garden. At Timberline the form from 1675 m. elevation thrives and is able to flower early enough to set ripe fruit almost every year. *Penstemon globosus* differs, therefore, from the likewise tetraploid *confertus* in being better adapted to higher altitudes.

SPECIATION IN THE SECTION ERIANTHERA

Penstemon, section *Erianthera*, is characterized by a woody habit, flowers that are strongly two-ridged or plicate in the floor of the throat, and anthers that are often quite concealed by a dense, woolly covering. The species are principally confined to the mountains of the Pacific Coast states but are also found in the northern Rockies. All the species that we have counted are diploid, $n=8$.

Two of the most unlike forms in the entire assemblage, which includes about eight species and seven subspecies, are represented along the transect of our transplant stations in the Sierra Nevada. These are *P. Newberryi* Gray and *P. Menziesii* Hook. ssp. *Davidsonii* (Greene) Pennell & Keck. Some of their differences are tabulated as follows:

Character	<i>P. Newberryi</i>	<i>P. Menziesii</i> ssp. <i>Davidsonii</i>
Elevational range in California	1000 to 3000 m.	2200 to 3800 m.
Flowering	Late	Early
Habit	Shrubby, many erect stems from the base 10 to 30 cm. tall	Scarcely woody, stems procumbent and creeping, forming mats, flowering shoots less than 10 cm. tall
Leaf blades	Oblong-elliptic, obtuse, 15 to 30 mm. long, bluntly serrate, glaucescent	Spatulate elliptic to oval, rounded at apex, 5 to 10 or 15 mm. long, entire, deep green
Racemes	3 to 10 pairs of flowers	1 to 3 pairs of flowers
Flowers	Rose pink, 18 to 25 mm. long, 5 to 7 mm. high	Deep blue to blue-purple, 25 to 40 mm. long, 8 to 10 mm. high
Corolla throat	Bearded with short rather stiff hairs	Bearded with longer flexuous hairs
Anthers	Exserted	Included
Staminodal beard . . .	Short, white	Longer, yellowish

In the vicinity of our alpine station *P. Newberryi* is near its uppermost limits, while *P. Menziesii Davidsonii* approaches its lower limit for the central Sierras. In two or three localities they grow together and hybridize freely. A selection of the hybrids found in

one of these colonies in Slate Creek Valley at 3100 m. is shown in figure 113, with the parental species beneath. To enable comparison of the mid-altitude form of *P. Newberryi* with that from alpine conditions, a specimen from Mather is shown at the lower left. Both plants of this species are garden specimens grown at Mather; the other individuals are from the wild. Even from the small hybrid sample of four plants that are illustrated, one can gain some impression of the free recombination of characters. A more comprehensive idea of the interchange may be gained from table 23, in which a few of the more outstanding characters have been tabulated from 182 plants—all that were in flower in one wild population. The parental classes are large (seemingly pure *Menziesii Davidsonii* is by far the most abundant class), but a very large number of recombinations is represented. This probably means that F_1 and later generations are both represented in this population, which showed no striking lack of vigor except a slight indication of reduced flowering in some of the hybrid recombinations.

The cytological behavior of the hybrids also reveals the close relationship between these plants that differ so widely in appearance. The pairing of all chromosomes in the hybrids is as regular as that in the parent species. This is illustrated by the chromosome drawings in figure 113. From this observation one should expect what he actually finds: the formation of good pollen and high fertility in the hybrids.

From this evidence we conclude that *P. Newberryi* and *P. Menziesii Davidsonii* are very closely related and doubtfully specifically distinct. In spite of the profound structural differences between them, we may justify their continued treatment as distinct species only because the genetic evidence has not been obtained under controlled conditions. Two pertinent distributional observations are, first, that the species very rarely meet and hybridize in nature, and second, that obvious recombinations have not been discovered outside of these relatively limited hybrid swarms, indicating that the recombined genes do not migrate far.

This demonstration of compatibility and intimate relationship is very impressive. It warns the systematist to hesitate before pronouncing as species forms in this section which fall far short of the morphological differentiation exhibited in the case just mentioned. *Penstemon Berryi* Eastw. and *P. rupicola* (Piper) Howell are cases



FIG. 113. Evidence of natural hybridization between the diploid *Penstemon Newberryi* and *P. Menziesii Davidsonii*.

Below, left: 1212-2, a mid-Sierran form of *P. Newberryi* from Mather, at 1400 m.

Center, left: 1213-1, *P. Newberryi* from Tenaya Lake, Yosemite Park, at 2500 m., representing the alpine form. Center, right: typical *P. Menziesii Davidsonii* from Mount Dana, Yosemite Park, at 3450 m.

Above: samples of a hybrid swarm at Gardisky Lake, near Tioga Peak, Mono County, at 3260 m. elevation. The 8 pairs of chromosomes and the equally regular pairing in the hybrids and the parental species are shown. Only the somatic chromosomes were observed in *Davidsonii*.

TABLE 23
 NATURAL POPULATION OF *PENSTEMON NEWBERRYI*, *P. MENZIESII* SSP. *DAVIDSONII*, AND
 INTERMEDIATES FROM NEAR TIMBERLINE STATION

Habit	Leaves	Flower color	Flower size	Stamens	Number of plants (total 182)
Erect	Serrate	Pink	Small	Exserted Included	13 Newberryi
			Large	Out In	
		Intermediate	Small	Out In	12 1
			Large	Out In	9 3
		Blue	Small	Out In	
			Large	Out In	
	Entire	Pink	Small	Out In	
			Large	Out In	1
		Intermediate	Small	Out In	3 1
			Large	Out In	4 1
		Blue	Small	Out In	4 1
			Large	Out In	3 2
Matted	Serrate	Pink	Small	Out In	2 1
			Large	Out In	1
		Intermediate	Small	Out In	9 2
			Large	Out In	5 2
		Blue	Small	Out In	
			Large	Out In	2
	Entire	Pink	Small	Out In	2
			Large	Out In	3 1
		Intermediate	Small	Out In	8
			Large	Out In	12 11
		Blue	Small	Out In	1 5
			Large	Out In	14 43 Davidsonii

in point. The former is a large-flowered *Newberryi* in appearance, with included anthers and a soft, instead of a stiff, beard on the palate. The latter is a mat with serrate, blue-glaucous foliage and rose-pink flowers. Even to the finer details *P. rupicola* in particular might now be expected to occur as a segregant from the cross *P. Menziesii Davidsonii* \times *P. Newberryi*. In nature it is found wholly to the north of *P. Newberryi* and is in the area occupied by *P. Menziesii Davidsonii*. Unquestionably both it and *P. Berryi* are natural units, but their specific status may now be questioned.

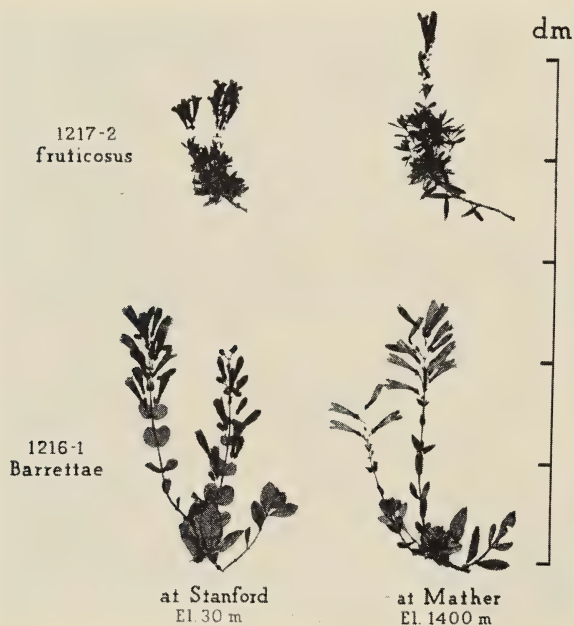


FIG. 114. Modifications in clones of *Penstemon fruticosus* and *P. Barrettae* at Stanford and Mather, both diploid, $n=8$.

Above: 1217-2, dug September 4, 1927, above Wallowa Lake, Wallowa County, Oregon, at 2000 m. The propagules were planted at Stanford in 1929, and at Mather in 1928; the specimens were taken in 1931.

Below: 1216-1, dug August 29, 1927, at Vila, Klickitat County, Washington, at 250 m. The propagules were planted at Stanford in 1929, and at Mather in 1928. The specimens were taken at Stanford in 1931, and at Mather in 1932.

TRANSPLANT RESULTS IN ERIANTHERA. Several species of this section have been employed in the varied-environment experiments from time to time. Stanford and Mather modifications of two of these are shown in figure 114. The upper clone is of *P. fruticosus* (Pursh) Greene, dug above Wallowa Lake in the Wallowa Mountains, north-

eastern Oregon, at 2000 m. elevation. The most interesting result obtained from this species, when it was moved considerably south of its natural distribution, was its obvious inability to flower successfully regardless of the altitude at which it was tried. It survives well at Mather (ten years and more) but rarely blooms; when flowers are produced they are few in number. At Stanford the species likewise remains vegetative most of the time, but a few flowers were produced two consecutive seasons on the clone illustrated. This clone also has been tried at Timberline, where it survived for three years but failed to flower. Very little vegetative modification has been evident in this species.

The lower clone in figure 114 is of *P. Barrettae* Gray, from hot, rocky cliffs above the Columbia River, in Klickitat County, Washington. The Stanford and Mather modifications differ strikingly in width of the cauline leaves and bracts. The much wider leaves at Stanford are also considerably thicker than those at Mather. This is the reverse of *Zauschneria*, in which the widest leaves were produced at Mather. This species grows well at Stanford but succeeds very poorly at Mather, where it is obviously near its threshold for survival. As would be expected from the character of the species and its low native habitat, it died promptly when tried at Timberline.

Penstemon Newberryi and *P. rupicola* are examples of stable transplants. The former, from the Sierra Nevada, thrives better at Mather than at Stanford; but the latter, from the banks of the Columbia River at a low elevation, follows the reverse pattern for success and survival. No striking modifications have been observed in these species.

TRANSPLANT RESULTS IN OTHER SPECIES

Evidence has been gathered bit by bit from many species, representing several other sections of *Penstemon*, which indicates that a wide range of problems are to be found in this genus. Only a few additional examples may be shown here.

One of the most complex sections in the genus is known collectively as the *Glabri*. Its members are common throughout the western United States at almost all elevations. Three of these are shown in figure 115; all are diploids, $n=8$. In the lower row are *Penstemon glaber* Pursh var. *alpinus* Gray, as dug at Florissant, Colorado, and

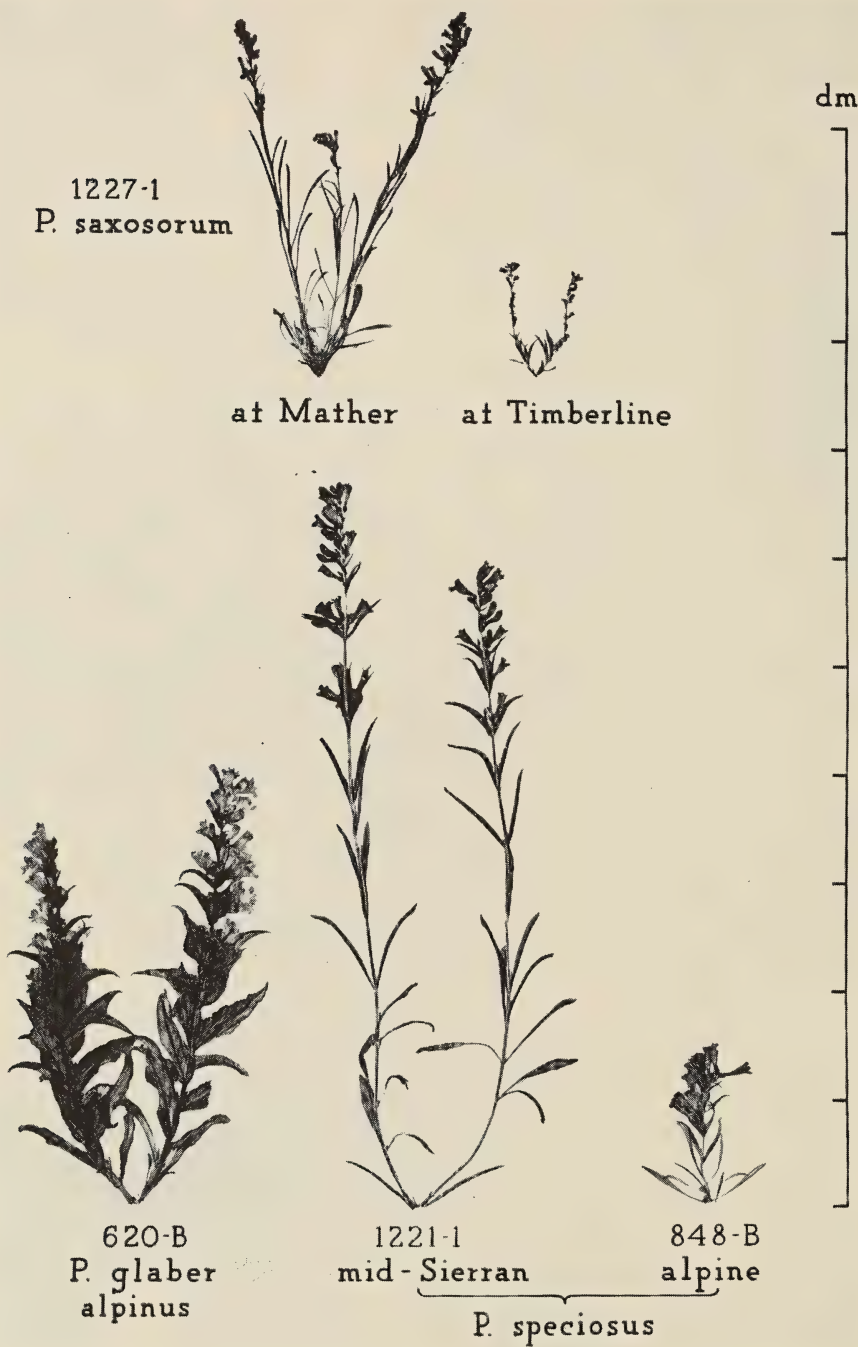


FIG. 115
(Legend on opposite page)

two very unlike races of *P. speciosus* Dougl., from California. These two species have been confused in some western floras but have several distinctive floral characters, and their distributions are very distinct. The mid-altitude race of *P. speciosus*, 1221-1, from the base of Yuba Pass, Sierra County, and the high-alpine race, 848-B, from Tioga Peak, near our alpine station, appear to be as morphologically unlike as several pairs of species in this section, but they are connected through a series of intergrades.

The two upper plants in figure 115 are members of a clone of *P. saxosorum* Pennell, originally from North Park, Colorado, showing Mather and Timberline modifications. The Mather propagules of this species all showed a moderate increase in size over the original individuals, but the Timberline reduction is extremely marked. The only propagule set at that station survived only a little more than one year.

Another large section of *Penstemon* is known under the collective name of *Coerulei*. Representative of this is another diploid ($n=8$), *P. pachyphyllus* Gray ssp. *congestus* (Jones) Keck, shown in figure 116 as it grows at the three transplant stations. This culture came from Sawtooth, Salina Canyon, Wasatch Mountains, central Utah, in the *Artemisia tridentata* association. It is typical of its section in having thick, blue-glaucous foliage. The modifications at the three stations are quite striking. At Stanford there is a marked dwarfing effect as compared with the modification at Mather. At Timberline the plant grows rather tall and flowers, but there is insufficient time remaining to enable it to ripen seed. A notable feature of this species is that it stays evergreen, not only at Stanford, but at Mather and Timberline as well! The thick, succulent leaves appear to remain functional at all stations throughout the winter. It survives remarkably well at all three stations.

FIG. 115. Representative *Penstemons* of the section *Glabri*, all diploid, $n=8$.

Above: a clone of *P. saxosorum* from Camp, Jackson County, Colorado, at 2600 m. The division at Mather became well established, but the one at Timberline, planted a year before the specimen was taken, became dwarfed and weak.

Below, left to right: 620-B, *P. glaber* var. *alpinus* from Florissant, Teller County, Colorado, at 2500 m.; 1221-1, a mid-Sierran form of *P. speciosus*, from Blairsden, Plumas County, California, at 1340 m., and 848-B, an alpine race from Tioga Peak, Mono County, California, at 3300 m. Plant 1221-1 is from a Mather garden, the others as dug.



FIG. 116. A clone of *Penstemon pachyphyllus* at three altitudes. Diploid, $n=8$.

This plant, 1229-1, was dug June 1930, near Sawtooth, Sevier County, Utah, at 2300 m. The propagules were planted at Stanford and Timberline in 1934, and at Mather in 1931. The specimens were taken in 1935.

CYTOLOGICAL INVESTIGATIONS

Cytological fixations have been made in *Penstemon* as opportunity has offered, in the experiments and on field trips, so that a large amount of material is now embedded awaiting final study. Many counts have already been made, but in the following lists counts are given only for those sections that have been mentioned in the preceding text.

CHROMOSOME NUMBERS OF PENSTEMON

Subsection Proceri

Penstemon procerus:

Diploid forms:

1251-1, *aberrans* form, Puffer Lake, Beaver Co., Utah, $n=8$.

1251-2, *aberrans* form, Cottonwood Canyon, E. of Fairview, San Pete Co., Utah, $n=8$.

1249-11, Farrington's, Mono Co., California, $2n=16$.

- F. 1822 (Clausen), *heterodoxus* form, Slate Creek Valley, Mono Co., $n=8$.
1248-1, *heterodoxus* form, Tioga Pass, $2n=16$.
1248-2, same, $2n=16$.
1247-2, Tuolumne Meadows, $2n=ca. 16$.
1244-4, Aspen Valley, Yosemite Park, $n=8$.
1245-1, same, $n=8$.
1243-4, Miguel Meadows, Tuolumne Co., $2n=16$.
1246-1, Mineral King, Tulare Co., California, $n=8$.
1017-2, form like *cinicola* but with rosette, East Lake, Paulina Mts., Deschutes Co., Oregon, $2n=ca. 16$ and $n=8$.
Keck 3693, Silver Lake, Lake Co., Oregon, $2n=16$.
Keck 3691, 20 mi. SE. of Lapine, Lake Co., Oregon, $n=8$.
Keck 3652, summit between Unity and Austin, Grant Co., Oregon, $n=8$.
Keck 3643, 6 mi. W. of Unity, Baker Co., Oregon, $n=8$.
Keck 3622, 3 mi. S. of Baker, Baker Co., Oregon, $n=8$.
Keck 3534, Liberty, Kittitas Co., Washington, $2n=16$.
1252-1, *Tolmiei* form, Mt. Hood, Oregon, $2n=16$.

Tetraploid forms:

- 1250-1, Camp, Jackson Co., Colorado, $n=16$ (some quadrivalents).
1249-1, form named *P. pratensis* Greene, possibly distinct, Clover Valley, 12 mi. S. of Wells, Nevada, $2n=ca. 32$.

Penstemon cinicola:

- Keck 3690, Lapine, Deschutes Co., Oregon, $n=16$ (chromosomes densely glomerated in first metaphase).

Penstemon confertus:

- 1242-2, Meacham, Umatilla Co., Oregon, $n=16$ (some quadrivalents).
Keck 3605a, same, $n=16$ (some quadrivalents).
Keck 3605, same, $n=16$ (some quadrivalents).

Penstemon globosus:

- 1239-4, Wallowa River, above Wallowa Lake, Wallowa Co., Oregon, $2n=32$.

Penstemon aggregatus:

- 1240-2, Salina Experiment Station, Sevier Co., Utah, $2n=32$.

Penstemon cinereus:

- Keck 3684, Bend, Deschutes Co., Oregon, $n=8$, $2n=16$.
S. 342, near Glenwood, Klickitat Co., Washington, $n=8$.

Penstemon humilis:

- Keck 3662, 4 mi. W. of Dixie Pass, Grant Co., Oregon, $n=8$.
Keck 3657, Dixie Pass, $n=8$.

Penstemon pruinosus:

- Keck 3570, S. of Lind, Adams Co., Washington, $2n=16$.

Penstemon albertinus:

- 1234-1, Montana, $2n=16$.

Penstemon virens:

1241-1, 10 mi. S. of Colorado Springs, Colorado, $n=8$.

1241-2, same, $n=8$.

Penstemon deustus:

Keck 3606, Emigrant Hill, Umatilla Co., Oregon, $n=8$.

Penstemon Rattanii:

Keck 3410, N. of Gold Beach, Rogue River, Curry Co., Oregon, $n=8$.

Penstemon Rattanii Kleei:

Keck 4569, Mt. Madonna, Santa Clara Co., California, $n=8$.

Penstemon minor:

1235-1, Mt. Ashland, Jackson Co., Oregon, $n=8$.

Penstemon ovatus:

1233-1, Cape Horn, Skamania Co., Washington, $2n=16$.

1233-2, same, $n=8$.

Penstemon Wilcoxii:

S. 344-1, Latah Co., Idaho, $2n=ca. 32$ (or more).

1236-1, *pinetorum* form, Bingen, Klickitat Co., Washington, $n=ca. 16$
($2n=31?$, $15 + 16$ in second meiotic metaphase).

Keck 3486, *pinetorum* form, Goldendale, Klickitat Co., Washington, $n=16$
(no quadrivalents).

Penstemon euglaucus:

1237-1, Cloud Cap Inn, Mt. Hood, Oregon, $2n=48$.

Penstemon attenuatus:

Keck 3600, Emigrant Springs, Umatilla Co., Oregon, $n=ca. 24$ ($n=22$ to
24 counted in second metaphase).

Keck 3601, same, $n=24$ ($23_{II} + 2_I$); multivalent association.

*Section Erianthera**Penstemon fruticosus:*

1217-2, above Wallowa Lake, Wallowa Mts., Wallowa Co., Oregon, $n=8$,
 $2n=16$.

1217-3, same, $2n=16$.

1218, same, $2n=16$.

Penstemon Barrettae:

1216-3, Vila, Klickitat Co., Washington, $n=8$.

Penstemon Newberryi:

1214-1, Mt. Shasta, California, $n=8$.

S. 103-1, same, $n=8$, $2n=16$.

Clausen 1104, base of White Mt., Slate Creek Valley, Mono Co., California,
 $n=8$.

Clausen 1137, Slate Creek Valley, $n=8$.

1213-1, Tenaya Lake, Yosemite Park, $n=8$.

1212-1, Mather, $n=8$.

Penstemon Menziesii typicus:

S. 336-1, Mt. Baker, Whatcom Co., Washington, $2n=16$.

Penstemon Menziesii Davidsonii:

S. 339-1, Mt. Hood, Oregon, $2n=16$.

Clausen 480, Saddlebag Lake, Mono Co., California, $2n=16$.

Penstemon Menziesii Davidsonii \times *Newberryi*:

Clausen 1104a, base of White Mt., $n=8$ (regular pairing); four series all had regular tetrads and pollen.

1211-13 to -18, Gardisky Lake, Tioga Peak, Mono Co., $2n=16$.

S. 305-2, 307-1, and -2, same, $2n=16$.

Penstemon rupicola:

1215-3, Mitchells Point, Hood River Co., Oregon, $n=8$, $2n=16$.

Section Nothochelone

Penstemon nemorosus:

1184-1, Clark Co., Washington, $n=15$, $2n=30$.

Keck 4821, Poker Flat, Siskiyou Mts., Del Norte-Siskiyou county line, California, $n=15$ (homotypic metaphase), $2n=15 + 15$ (heterotypic anaphase).

Subsection Glabri

Penstemon glaber alpinus:

620-A, Florissant, Teller Co., Colorado, $n=8$.

Penstemon speciosus:

Keck 3571, S. of Lind, Adams Co., Washington, $n=8$, $2n=16$.

Keck 3658, Dixie Pass, Grant Co., Oregon, $n=8$.

Keck 3679, Ochoco, Crook-Wheeler county line, Oregon, $n=8$.

1223-1, Klamath Falls, Oregon, $2n=16$.

1221-1, Blairsdén, Plumas Co., California, $n=8$.

1222-1, Yuba Pass, Sierra Co., $2n=16$.

848-C, Gardisky Lake, Tioga Peak, Mono Co., $2n=16$.

Penstemon saxosorum:

1227-1, Camp, Larimer Co., Colorado, $2n=16$.

Penstemon subglaber Rydb.:

1225-1, Salina Canyon, Sevier Co., Utah, $n=8$.

Penstemon cyananthus Hook.:

1228-2, Big Cottonwood Canyon, Salt Lake Co., Utah, $n=8$.

Penstemon strictus Benth.:

1226-1 and 1456-1, North Park, Jackson Co., Colorado, $n=8$, $2n=16$.

*Subsection Coerulei**Penstemon pachyphyllus congestus*:1229-1, Sawtooth, Salina Canyon, Sevier Co., Utah, $n=8$.*Penstemon secundiflorus* Benth.:1456-1, Centennial, Albany Co., Wyoming, $2n=16$.621-B, south of Colorado Springs, El Paso Co., Colorado, $n=8$.

SYSTEMATIC NOTES

PENSTEMON section **Nothochelone** Pennell & Keck sect. nov.Type species *P. nemorosus* (Dougl.) Trautv.**Penstemon cinicola** Keck sp. nov.

Herba perennis glaber (saltem caules apud basem minute puberuli); caulibus herbaceis e basi suffrutescente erectis 15–35 cm. altis gracilibus foliosis; foliis radicalibus fere nullis, caulinis linearibus moderate recurvis integerrimis 25–55 mm. longis 2–4 mm. latis, floralibus lanceolati-subulatis attenuatis; thyrsos stricto contracto; cymis subsessilibus multifloris 3–6 geminis; calyce 1.6–2 mm. longo, lobis obovato-oblongis truncatis vel mucronatis late scarioso-marginatis; corolla purpureo-coerulea 7.5–9 mm. longa declinata, palato barbato; antheris glabris inclusis; filamento sterili apud apicem barbato.

Type, from among tussocks of grass and sedge on bare volcanic sand, in openings of *Pinus contorta* forest just north of Lapine, Deschutes County, Oregon, at 1285 m. (4225 ft.) elevation, June 23, 1935, *Keck & Clausen 3690* (Dudley Herbarium of Stanford University); isotypes Academy of Natural Sciences, Philadelphia, and Carnegie Institution. This collection is tetraploid.

We refer the following collections from Klamath County, Oregon, here: 20 miles south of Lapine on road to Silver Lake, *Keck & Clausen 3692* (U. of Calif., Carnegie Inst., Phila., Pomona, Stanford, U. S. Nat. Herb.); Odell Lake, *Howell 6911* (Calif. Acad., Carnegie Inst.); Annie Creek valley, near south entrance to Crater Lake National Park, *Applegate 11113* (Carnegie Inst., Stanford).

Penstemon globosus (Piper) Pennell & Keck comb. nov.*P. confertus* var. *globosus* Piper, Bull. Torr. Club 27:397, 1900.**Penstemon Rattanii** Gray ssp. **typicus** Keck nom. nov.*P. Rattanii* Gray, Proc. Amer. Acad. 15:50, 1879.

Penstemon Rattanii ssp. **Kleei** (Greene) Keck comb. nov.

P. Kleei Greene, Bull. Torr. Club 10:127, 1883.

P. Rattanii var. *Kleei* Gray, Syn. Fl. 2(1):441, 1886.

Penstemon minor (Gray) Keck comb. nov.

P. Rattanii var. *minor* Gray, Proc. Amer. Acad. 15:50, 1879.

Penstemon Menziesii Hook. ssp. **Davidsonii** (Greene) Pennell & Keck comb. nov.

P. Davidsonii Greene, Pittonia 2:241, 1892.

P. Menziesii (var.) *Davidsonii* Piper, Mazama 2:99, 1901.

P. Menziesii f. *Davidsonii* G. N. Jones, Univ. Washington Publ. Biol. 5:226, 1936.

VIII

THE ACHILLEA MILLEFOLIUM COMPLEX

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While *Achillea* has not been so extensively studied in our experiments as *Potentilla glandulosa*, *P. gracilis*, or *Zauschneria*, it has nevertheless proved to be one of the most fruitful forms in demonstrating the kinds of differentiation that may take place in species that occupy a wide geographical range. The varied-environment studies have shown, first, that different ecotypes are fitted to special environments; second, the range of modifications possible from transplanting to different altitudes; and third, something of the extreme physiological complexity of a group that has been able to establish itself throughout most of the Northern Hemisphere. Moreover, cytological studies and some genetic evidence at critical points have clarified our conception of the specific limits between the members of this complex.

GENERAL RELATIONSHIPS AND TAXONOMY

The relationships between the very diverse but obviously allied plants in this group have not yet been fully determined. We have enough evidence, however, to provide strong clues as to the organization of this group; therefore we shall outline our present conclusions, leaving to future investigations the task of painting the picture in greater detail.

An example of the great diversity seen along our transplant transect is given in figure 117. All these plants were growing in a uniform garden at Stanford, and were photographed the same season, so the differences are hereditary. A maritime form is common in sandy situations along the immediate California coast. As one goes inland even but a short distance, this is replaced by a taller, more slender plant, a very common and variable form throughout the Coast Ranges (not illustrated). In the Sierra Nevada, forms like the three



FIG. 117. Representatives of regional races of *Achillea* from a transect across California in a uniform garden at Stanford.
Left to right: 1313-3, *A. borealis arenicola* from the coast at Montara, San Mateo County, near sea level, $n = 27$; 1315-4, a mid-Sierran form of *A. lanulosa* from near Mather at 1400 m., $n = 18$; 2459-1, a subalpine form of *lanulosa alpicola* from Le Conte Falls, Yosemite Park, at 2150 m., $n = 18$; and 1316-1, an alpine form of *lanulosa alpicola* from near Timberline at 3050 m., $n = 18$. Photographs taken in 1937, all shown to the same scale.

right-hand specimens and nearly every intergrade between them may be found. Even within single populations one finds considerable variation, but never so great as that between any two of the forms illustrated.

We naturally turn next to the question, How many species are there in this complex? From the morphological viewpoint it is almost impossible to arrive at a satisfactory delimitation of the natural units, because the number of characters that vary is too great and the intergradation is too complete. A survey of a large series of herbarium specimens leaves one with the impression that intergrades exist between all the American forms, and that if natural units occur their precise definition can at best only be approximated. In this situation it is obvious that such experimental procedures as those which proved to be successful in *Zauschneria* are needed. For lack of time, we have been unable to carry our investigations in *Achillea* so far, but the evidence obtained permits us to draw some tentative conclusions.

The key to the species question in *Achillea* lies in the cytogenetic characteristics of its members. This complex resolves itself into at least three species, each composed of a series of ecotypes. Two species are hexaploid, with 27 pairs of chromosomes, while the third is tetraploid, and has 18 pairs. As yet, no diploids have been discovered in this complex.

One of the hexaploid species, *Achillea millefolium* L., is Eurasian, but has been widely introduced elsewhere, as in the eastern United States, where it is well established. It is difficult to characterize briefly the morphological distinctions between this species and the western American forms. In general it has fewer secondary divisions of the leaves, and these are divided commonly into relatively few linear-lanceolate, instead of into numerous linear-subulate, ultimate segments. The heads of *millefolium* are usually smaller. These distinctions do not always appear obvious, but the morphological confusion is greatest between this hexaploid and forms of the tetraploid species.

The second hexaploid species is *Achillea borealis* Bong., which occurs along the Pacific Coast of North America from Alaska to Baja California. Three ecotypes are now recognized within this species. One is maritime and apparently limited to the coastal dunes in California and perhaps Oregon. It is recognized by the increased num-

ber and thickness of the leaf segments, characteristics that are retained when the plants are moved into the transplant gardens. This ecotype is ***A. borealis* ssp. *arenicola*** (Heller) Keck comb. nov. (*A. arenicola* Heller, *Muhlenbergia* 1:61, 1904; type locality, sand-hills at the upper end of Bodega Bay, Sonoma County, California). It is illustrated by the plant 1313-3, in figure 117.

The second ecotype is also a morphologically recognizable subspecies, ***A. borealis* ssp. *californica*** (Pollard) Keck comb. nov. (*A. californica* Pollard, *Bull. Torr. Club* 26:369, 1899). It occurs in the Coast Ranges, in the lowest foothills of the Sierra Nevada, and probably along the western flank of the Cascades in Oregon and Washington, from Vancouver Island southward to Sierra San Pedro Martir, Baja California. It is a taller, more slender, and thinner-leaved form than ssp. *arenicola* (see 1313-4, fig. 118).

The third ecotype is northern, ***A. borealis* ssp. *typica*** Keck nom. nov. (*A. borealis* Bong., *Mem. Acad. St. Petersburg* VI, 2:149, 1832). It is found from the Arctic Coast of Yukon Territory (Herschel Island) westward around Alaska and to the westernmost Aleutians, and southeastward along the Pacific perhaps as far south as Vancouver Island. The type of this species came from Sitka. This ecotype differs from the preceding in that the inflorescence is crowded or subtended by foliage leaves and the margin of the involucre bracts is dark brown or blackish (see 2443-1, fig. 118).

The tetraploid species, *Achillea lanulosa* Nutt., presents as much if not more morphological variation than the hexaploid. Examples are the three right-hand specimens in figure 117. It covers a wide territory in the western United States and Canada, yet we have been unable to distinguish more than two subspecies by a survey of much herbarium material. The variation, otherwise, appears to be too much at random. Experiments, however, have shown that more than one ecotype is involved in each of these. The form of mid-altitudes in the Sierras and the Great Basin mountain ranges is ***A. lanulosa* ssp. *typica*** Keck nom. nov. (*A. lanulosa* Nutt., *Jour. Acad. Phila.* 7:36, 1834). The type locality is the banks of the Kooskoosky (Clearwater River, Idaho). It is found from the Cascades and Sierras eastward to the Rockies of Wyoming and Colorado, and from the mountains of New Mexico northward to northern Alberta. *Achillea lanulosa typica* may occur in Yukon Territory and even Alaska, but as it can be distinguished from some forms of

borealis with certainty only by cytological means, and as such investigations have been limited to date, we are uncertain of the geographical limits of the two species.

In the subalpine and alpine zones in the Cascade Range, the Sierra Nevada, and the Rocky Mountains, we find the second subspecies of this species, ***Achillea lanulosa* ssp. *alpicola*** (Rydb.) Keck comb. nov. (*A. lanulosa* [var.] *alpicola* Rydb., Mem. N. Y. Bot. Gard. 1:426, 1900; type locality, Teton Forest Reserve, Wyoming. *A. subalpina* Greene, Leaflets 1:145, 1905). It is distinguished by its low stature, the narrow leaves, and the often blackish margin of the involucre bracts.

Although we have attempted to establish a correlation between cytological and morphological characters through herbarium studies, the variation within each species is greater than any morphological difference between the species. Chromosome counts by Turesson (1938) and ourselves have established the distribution of *borealis* in the Coast Ranges and the lowest Sierran foothills, and at Seward, Alaska; they have similarly shown that *lanulosa* occurs in the higher foothills to high altitudes in the Sierras, in the Great Basin region, eastern Washington and Oregon, and in the Peace River district east of the Canadian Rockies.

A plant of the hexaploid European *A. millefolium* L. from Denmark failed to produce offspring when crossed with *A. borealis* from California having the same chromosome number—an indication that the American species is distinct from the European. Moreover, the morphological differences between these two are appreciable.

DIFFERENTIATION INTO ECOTYPES

Each of the three species outlined above has a wide geographical distribution, and occupies a variety of environments. That they all have distinct ecotypes fitted to these environments is clear from the evidence at hand.

ACHILLEA BOREALIS. Results from the transplant experiments show a striking difference in the reactions of two latitudinal ecotypes—one from Seward, Alaska, and the other from the California Coast Ranges. This is illustrated in figure 118, showing the two at the three transplant stations.



FIG. 118. Modifications at three altitudes in two clones representing latitudinal ecotypes of *Achillea borealis*. Both are hexaploid, $n = 27$. Above: ssp. *typica*, 2443-1, from Seward, Alaska, near sea level; all the propagules of this seedling were planted in 1935. Below: ssp. *californica*, 1313-4, from Berkeley Hills, California, at 150 m.; the propagules were planted at Stanford in 1929, and at Mather in 1929, and at Timberline in 1926; repeated plantings at Timberline failed to survive. Photographed in 1937 and shown to the same scale.

It is obvious that the Alaskan plant (2443-1)¹ grows well at all three stations despite the great contrasts in climate. It is modified conspicuously, however: at Timberline it is much dwarfer than at Mather, having shorter stems and smaller leaves, and its bulk is greatly reduced. The Stanford specimen is intermediate in appearance between the other two. It is noteworthy that the parent plant of 2443-1, when collected in Alaska, most resembled the Mather modification, as evidenced by the original herbarium specimen.

The transplant of ssp. *californica*, 1313-4, from Berkeley, reacted in a very different way. It failed completely to survive at Timberline. Others from the central California coast likewise invariably succumbed, if not after the first winter, then after the second. The Berkeley plant reached its greatest height, produced the largest basal leaves, and became most massive at Stanford, not at Mather, a modification doubtless associated with the contrasts in the seasons at the two stations.

A total of twenty-seven plants of the Alaskan race of *Achillea borealis* were grown in the Stanford garden in addition to three individuals used as transplants. They were all early and characteristically low, although varying between 19 and 38 cm. in height, and were morphologically distinct from any representatives of California *borealis*. They lived from 1934 to 1936, but gradually became weak after that time, so that in 1939 not one remained alive. The warm, dry summers were deleterious to them and they were never very floriferous. It took more than a year to bring them to the flowering stage.

ACHILLEA LANULOSA. The differences mentioned in the latitudinal ecotypes of *borealis* are matched by an even more spectacular altitudinal differentiation in *lanulosa* along the transplant transect, as shown in figure 119. Here clones of mid-Sierran, subalpine, and alpine origin are shown as they appear at the three stations.

In making the horizontal comparisons, one gets the general picture of the modifications and climatic reactions at the transplant stations. The Mather plant grows even taller and more luxuriantly at Stanford than at Mather, while at Timberline it is barely able to produce a few basal leaves in the protected slope garden. These reactions

¹ This transplant is a seedling grown from akenes kindly furnished by Dr. Hultén from a herbarium specimen (*Hultén 7808*) deposited at the University of Lund, Sweden.

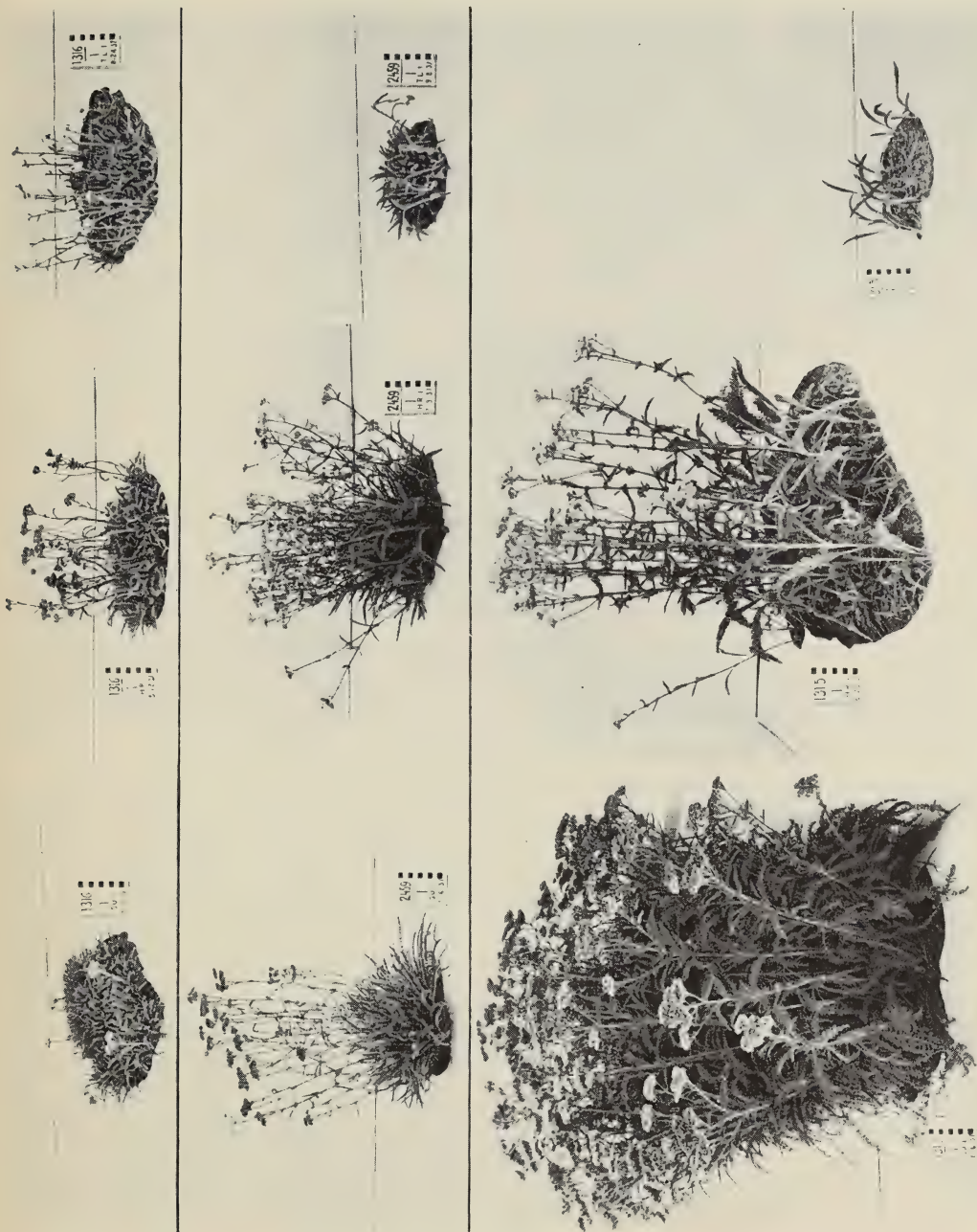


FIG. 119. Modification at three transplant stations in three clones representing altitudinal ecotypes of *Achillea lanulosa*. All are tetraploid, $n=18$. *Top row:* an alpine, 1316-1, dug September 12, 1929, near Timberline station at 3260 m. The propagules were planted at Stanford and Mather in 1930, and at Timberline in 1933. *Center row:* a subalpine, 2459-1, dug July 16, 1934, near Le Conte Falls, Yosemite Park, at 2165 m. All these propagules were planted in 1935. The stems on the Timberline clone member have been killed by frost. *Bottom row:* a mid-Sierran plant, 1315-1, dug August 27, 1933, near Mather at 1425 m. All these propagules were planted in 1934. All photographs taken in 1937, and reproduced to same scale.

remind one of those already seen in *A. borealis* ssp. *californica*. The subalpine form of *lanulosa* grows remarkably well at all three stations, but it attains its greatest vigor at Mather. At Timberline it survives well, producing a vigorous set of rosette leaves and many young stems—a futile development, however, because they mature so slowly that they are killed by frosts before they flower. Only the alpine plant is able to reach maturity at Timberline, but, like the subalpine, it attains its greatest vigor at Mather.

In the vertical comparisons in figure 119 one sees how clones of the three races appear to an observer at any one of the transplant stations. The differences seen between them at Stanford are not the same that one would see at Mather. At Timberline the picture is again very different: the Mather clone is reduced to a dwarf rosette, overtopped by the taller, flowering alpine form. At all three stations, however, it would be obvious that the clones are of a different heredity.

ACHILLEA MILLEFOLIUM. An example of ecotype differentiation in this European species is seen in figure 120, which shows a maritime and woodland form² from Denmark growing in a uniform garden at Stanford. These two differ somewhat in their reactions to transplanting, as well as in their morphology in a standard environment. In this case the morphological differences between the two ecotypes are scarcely as striking as in the examples given above for *borealis* and *lanulosa*—a fact that might be expected from the greater contrast between the original habitats of the ecotypes used in the previous illustrations. It is of interest that the morphological difference between the maritime and inland ecotypes of *millefolium* in Denmark parallels that between the maritime and inland forms of *borealis* in California.

Both of these Danish forms were grown as seedlings in California. The maritime plant, 2442-1, came from a population of low plants on a sandy and exposed shore on the west side of the island of Sjaelland. The woodland form, 1808-1, was from the border of Geels Forest, ninety kilometers away in the northeastern part of the same island. At Stanford the two forms differ remarkably in the time they require to begin flowering. Most of the twenty-nine plants of

² The seeds of the woodland form were kindly furnished by Professor Dr. Ö. Winge, Director of the Department of Physiology, Carlsberg Laboratory, Copenhagen.



FIG. 120. Maritime (left) and woodland (right) forms of *Achillea millefolium* in a uniform garden at Stanford. Both are hexaploid, $n=ca. 27$.

Plant 2442-1 is from the seacoast south of Korsör, Sjaelland, Denmark, while 1808-1 is from Geels Forest, 20 km. northeast of Copenhagen at 50 m. Both were set in 1934. The photographs, taken in 1937, are reproduced to the same scale.

the maritime ecotype bloomed four months after they had been sown, but the five plants of the woodland ecotype did not flower freely before their third year. However, clone members at Mather and Timberline flowered the second year. At Stanford the longest stems vary between 13 and 30 cm. in length in the maritime population (as compared with 10 to 20 cm. in the native habitat), but are longer in the woodland population, varying between 26 and 65 cm. Both are erect, but the maritime consistently flowers one month earlier than the other. The evidence, then, all points to the conclusion that the two represent different ecotypes.

In his transplant cultures Turesson (1930a) found marked differences in height between Siberian and Swedish woodland ecotypes of *Achillea millefolium*, but no differences in earliness. The habitat of his inland ecotype from Stehag is only sixty kilometers from that of our Danish inland form. His description of this form as it grew in the Åkarp garden shows it to be very like the Danish plant growing at Stanford (fig. 120). This suggests that the Stanford and Åkarp modifications of this ecotype are quite alike, even in height. Such a result is surprising in view of the great difference in climate between the two places, and the observed large reductions in size of other

plants of northern latitude when brought to Stanford, such as *Potentilla rupestris* (see fig. 10), and the Alaskan *Achillea borealis*.

Figure 121 illustrates the reactions of the Danish woodland ecotype of *Achillea millefolium* at the three transplant stations. The best development of this form is at Stanford, but it also thrives at Mather. At Timberline it survives very persistently, but has never approached maturity except in the first and unusually favorable year. In the meadow garden at Timberline there is a limited development of matted rosette leaves, so small that they are barely visible in figure 121 (lower right) even at the end of the growing season in September. In the slope garden (upper right) development proceeds further, even to the production of young flowering shoots. These are killed by frosts before the flowers have a chance to open.

From these examples it is apparent that the three species of *Achillea* considered—*borealis*, *lanulosa*, and *millefolium*—all have ecotypes that show different reactions at the transplant stations. It should not be forgotten, however, that individual variation within each ecotype may be appreciable, a fact that becomes evident even in the small samples represented by our transplants. For example, in the Californian and Alaskan forms of *borealis*, and in the mid-Sierran plants of *lanulosa*, variation in length of stems and basal leaves, and in time of flowering, is considerable, as is shown in table 24. These characters are tabulated for a number of individuals growing at Stanford, and the figures represent three-year averages. The "pentaploid" plant from Washington, D. C., listed at the bottom of table 24, is thought to be a form of *millefolium* introduced from Europe, but in view of its odd chromosome number ($2n=ca. 45$), we prefer to await more evidence before attempting to assign it to a species.

MODIFICATIONS AT TRANSPLANT STATIONS

While we have already surveyed some of the more salient results from the varied-environment studies in considering the differences between ecotypes, a more detailed study brings out additional facts of importance.

MODIFICATIONS IN FORM. An illustrated summary of the modifications of five ecotypes of *Achillea* at the transplant stations is shown in figure 122. The horizontal comparisons, in this case, show the

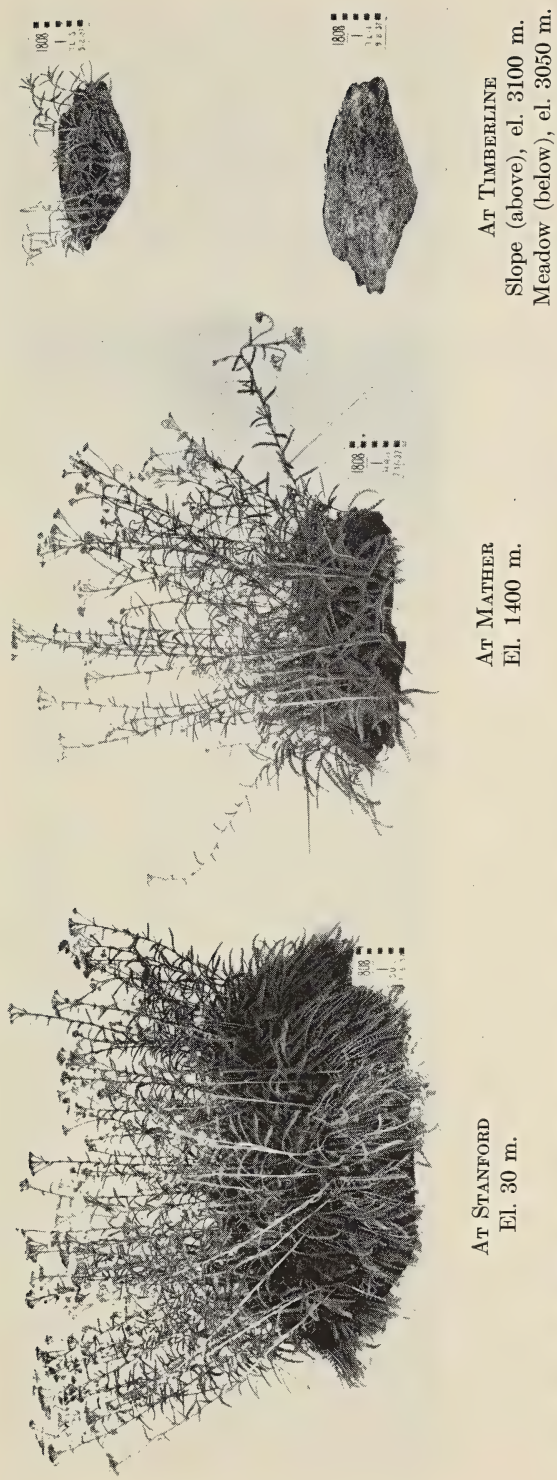


FIG. 121. Modifications at three altitudes in a clone representing the woodland ecotype of *Achillea millefolium* from Denmark. Hexaploid, $n = ca. 27$.
 Propagules of this plant, 1808-1, were planted at Stanford in 1934, and at Mather and Timberline in 1933. See figure 120 for history of plant.
 The photographs, taken in 1937, are reproduced to the same scale.

TABLE 24
 VARIATION IN *ACHILLEA* AT STANFORD
 (Data averaged from three years, 1935-1937)

Number and origin of plants	Longest stem (cm.)	Longest leaf (cm.)	Date of first flowers
<i>Achillea borealis</i> :			
CALIFORNIA COAST:			
1212-2, Half Moon Bay, 5 m.	95.0	47.7	May 3.0
1313-1, Pt. Montara, 5 m.	78.0	40.7	May 26.0
-2, Same.	59.0	37.0	May 12.3
-3, Same.	70.0	42.0	Jun. 4.0
-4, Berkeley, 150 m.	75.7	49.0	May 9.3
1314-1, Same.	102.3	48.3	May 7.0
1820-1, Morro Rock, 5 m.	103.7	48.3	May 24.3
2458-1, Asilomar, 5 m.	94.3	50.0	Jun. 3.5
-2, Same.	108.0	45.5	Jun. 10.0
-3, Same.	100.0	35.5	Jun. 7.5
Means.	88.6	44.4	May 23.1
ALASKA COAST:			
2443-1, Seward.	24.0	11.7	Mar. 30.0
-2, Same.	21.5	19.0	May 9.0
-3, Same.	16.3	18.7	Apr. 28.5
Means.	20.6	16.5	Apr. 22.5
<i>Achillea lamulosa</i> :			
MID-SIERRAN:			
1315-1, Mather, 1425 m.	86.0	36.3	May 7.3
-2, Same.	72.0	30.0	May 4.7
-3, Same.	66.7	31.7	May 6.3
-4, Mather, 1400 m.	74.7	26.3	May 25.0
-5, Mather, 1375 m.	65.3	24.3	May 17.7
Means.	72.9	29.7	May 12.2
SUBALPINE:			
2459-1, Le Conte Falls, 2165 m.	46.0	18.5	May 5.7
ALPINE:			
1316-1, Slate Creek Valley, 3260 m.	16.7	8.3	Jun. 22.3
-2, Same.	12.5	9.0	May 25.0
GREAT BASIN:			
2460-2, Mono Lake, 2100 m.	41.3	21.3	Jun. 6.0
<i>Achillea millefolium</i> :			
MARITIME:			
2442-1, Storebelt, Denmark, 3 m.	28.3	19.0	May 15.3
-2, Same.	25.7	20.0	May 10.0
WOODLAND:			
1808-1, Geels Forest, Denmark, 50 m.	65.7	24.0	Jun. 17.7
PENTAPLOID:			
1317-1, Washington, D. C.	116.0	43.0	May 28.3

differences between the ecotypes at one station, and the vertical rows show the modifications of a clone of each ecotype at the three stations. There are illustrated a plant of the maritime ecotype of *borealis* and representatives of four ecotypes of *lanulosa* from our Sierran transect.

It is noteworthy, first, that the maritime *borealis* with 27 pairs of chromosomes shows the same general modifications as the mid-Sierran ecotype of *lanulosa* with only 18 pairs. Both are tallest and most vigorous at Stanford, and both fail to produce more than a few rosette leaves at Timberline. They do show differential reactions, however, as in the relatively greater reduction in size and vigor of the maritime form at Mather as compared with the mid-Sierran. Moreover, as is shown below, the maritime form does not survive very well at the mid-altitude station, but the Mather form does.

Next, the three ecotypes of *lanulosa* from relatively high altitudes—the subalpine, alpine, and Great Basin ecotypes—thrive at all three stations. Only the alpine, however, is able to mature at Timberline; the other two never ripen seed there. The subalpine plant, 2459-1, shows the least modification of the three. It differs appreciably from the Great Basin plant in morphology and in its reactions, despite the fact that the two came from similar altitudes, the subalpine from 2150 m., the Great Basin from 1950 m.

From its morphological characters and its transplant reactions it is clear that the mid-Sierran form of *lanulosa* differs from its alpine relative far more than from the Coast Range or maritime ecotypes of *borealis*. In other words, the ecotypic differentiation within *lanulosa* runs a gamut of variation far in excess of the morphological and physiological differences between its mid-altitude ecotype and the geographically closest ecotype of *borealis*. This is despite the fact that the two species are barred from a free interchange of genes because of a difference in chromosome number.

The most striking modification that we have observed in *Achillea* is in the pentaploid form from Washington, D. C., collected by Dr. Hall in 1921. This individual, whose cytology was only recently investigated, has been under study in the gardens for eighteen years. Up to the time of the discovery of its pentaploid nature, it was assumed to be a European introduction of *A. millefolium*. The plant grows with extreme vigor at Stanford, attaining a height of a meter or more. Its very numerous, stiffly erect, sturdy stems and many

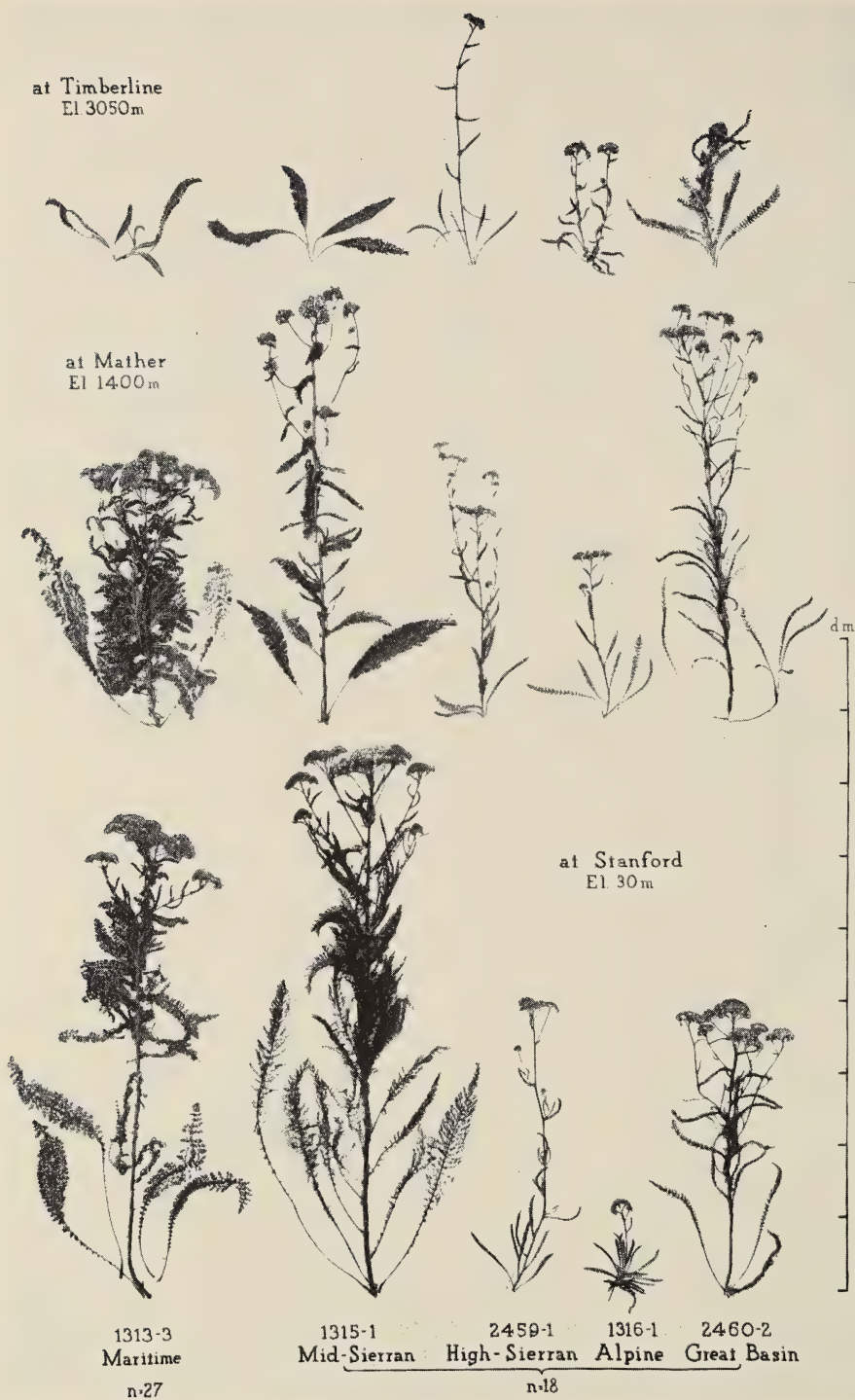


FIG. 122
(Legend on opposite page)

basal leaves mark it as one of the largest and most vigorous plants of *Achillea* in the Stanford garden. Clone members at Mather grow well year after year, but the stems are strikingly reduced in stature, as is shown in figure 123. At Timberline the plant persisted remarkably well for one originally from so mild a climate as that of Washington. The story of its struggle, decline, and finally its demise at the alpine station is illustrated in the figure.

The modifications at the transplant stations can be summarized statistically through such measurable characters as length of stems and size of basal leaves. Figure 124 shows in graphic form the lengths of stems of the various ecotypes, averaged for the seventeen plants listed in table 26. The most striking feature is the shortening of the stems of the pentaploid form at Mather as compared with Stanford, and a similar but less pronounced effect on the forms of *A. borealis* from the California coast. The Alaskan forms of *borealis* and the alpine and Great Basin forms of *lanulosa* are tallest at Mather, while the subalpine plant of *lanulosa*, together with the two forms of *millefolium* from Denmark, show no significant differences at the two lower stations. The mid-Sierran plants of *lanulosa*, on the other hand, are slightly but definitely taller at Stanford than in their native environment at Mather. At Timberline the plants with the longest stems are the subalpine and Great Basin forms of *lanu-*

FIG. 122. Modifications at three transplant stations in five clones representing altitudinal ecotypes and ecospecies of the California Achilleas. The lowest row consists of specimens grown at Stanford, the middle row at Mather, and the top row at Timberline.

Left to right: *A. borealis arenicola* from the California coast near sea level (1313-3), and Sierran races of *A. lanulosa* from 1425 m. (1315-1), 2165 m. (2459-1), 3260 m. (1316-1), and a Great Basin form from 2100 m. (2460-2).

Histories: 1313-3, dug near Montara Lighthouse, San Mateo County, October 26, 1923. The propagules were planted at Stanford in 1929 (having grown at Berkeley since 1923), at Mather in 1934, and at Timberline in 1933. Specimens taken in 1935.

1315-1, dug near Mather, August 27, 1933. The three propagules were planted in 1934 and specimens taken at Stanford in 1937, at Mather and Timberline in 1935.

2459-1, dug July 16, 1934, at Le Conte Falls, Yosemite Park. The three propagules were planted in 1935, and specimens taken in 1935 at Stanford, and in 1936 at Mather and Timberline.

1316-1, dug September 12, 1929, near Timberline station. The propagules were planted at Stanford in 1930, at Mather in 1935, and at Timberline in 1933. The specimens were taken at Stanford and Timberline in 1935, and at Mather in 1937.

2460-2, dug July 13, 1934, near Mono Lake, Mono County. The propagules were planted at Stanford in 1934, at Mather and Timberline in 1935. The specimens were taken in 1935 at Stanford, and in 1936 at Mather and Timberline.

losa. These, the alpine *lanulosa*, and the Alaskan *borealis* are the only ones that attain full height at the alpine station. All others, except *millefolium*, can be classed as nonsurvivors, as indicated by the broken line in the graphs.



FIG. 123. Modifications in a clone of a pentaploid *Achillea* at three transplant stations. This plant, 1317-1, was dug June 8, 1921, at Washington, D. C. The propagule at the left was grown at Berkeley until 1929, when it was moved to Stanford; the ones at Mather and Timberline are divisions from it planted in 1933. The specimens illustrated were taken at Stanford and Mather in 1935, and at Timberline in the years indicated.

Another method of regarding the modifications on a quantitative basis is given in figure 125, which shows the relative sizes of the basal leaves at the three transplant stations. It is evident that the leaves of Californian *borealis* and mid-Sierran *lanulosa* shrink conspicuously at Mather as compared with Stanford. On the other hand,

the plants of alpine *lanulosa* and Alaskan *borealis* show a striking modification in the opposite direction. At Timberline the leaves are all smaller than those produced at Mather, but the alpine and subalpine forms show much less reduction than the others. The modifications in leaf form show a marked parallel to those in stem length.

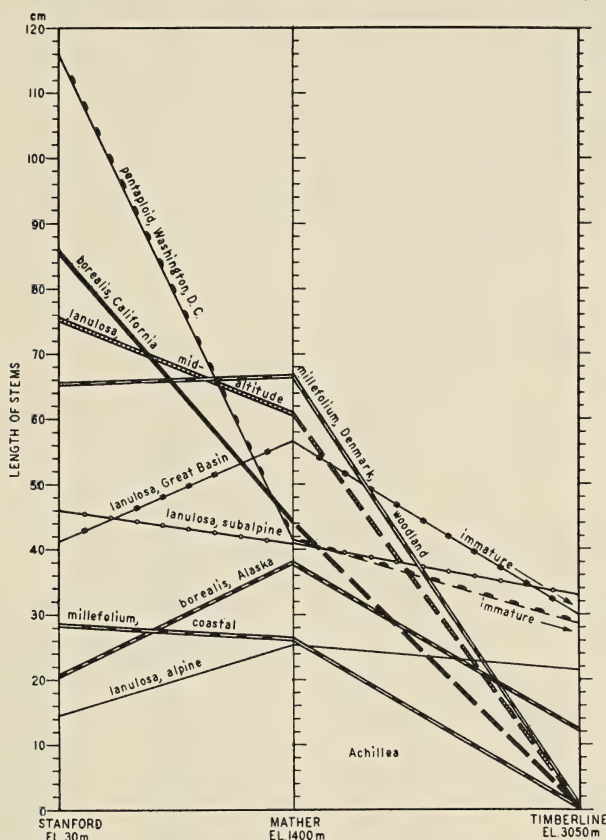


FIG. 124. Modifications at three altitudes in length of stems in clones representing ecotypes and ecospecies of *Achillea*.

Data graphed from three-year averages, 1935 to 1937, for the plants of each group listed in table 26. Broken lines indicate failure to survive at Timberline.

MODIFICATIONS IN TIME OF FLOWERING. It will be recalled from chapters II, III, and IV that the various ecotypes of *Potentilla* differ from each other greatly in their time of flowering, the alpiners being always earlier than the lowland forms. In most of the ecotypes approximately the same relative differences in earliness were observed at all three stations, so that the earliest at one station was also the

first to flower at the others, although coastal and mountain forms showed appreciable differences in rate of development at different stations.

The situation is not so simple in *Achillea* because we find more

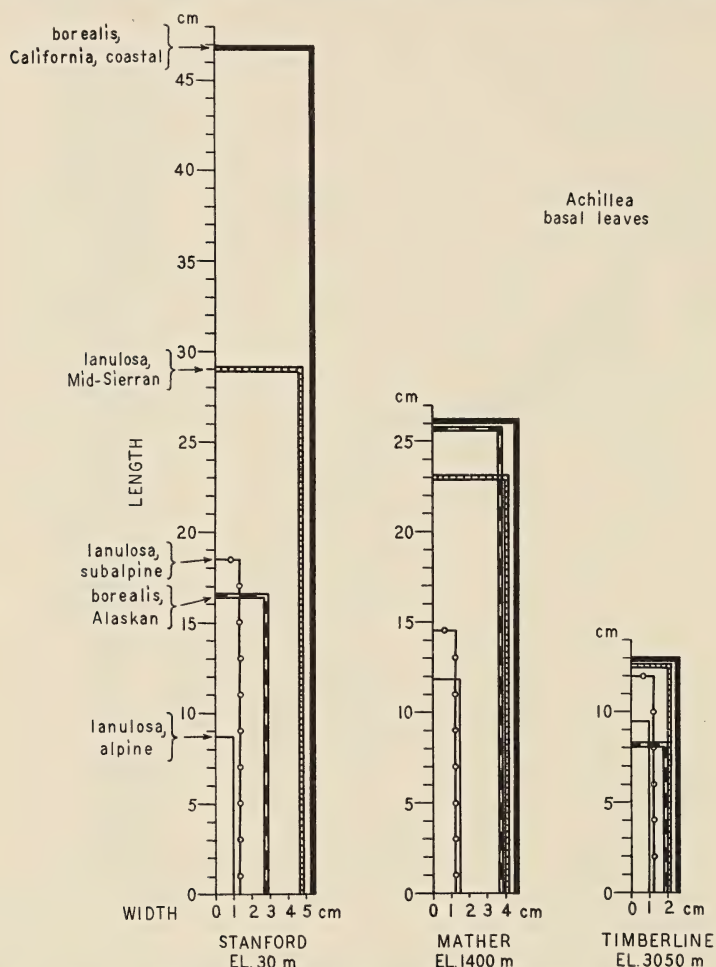


FIG. 125. Modifications at three altitudes in leaf sizes in clones representing ecotypes and ecospecies of *Achillea*.

Data graphed from four-year averages for the years 1934 to 1937 for the plants listed in table 26.

pronounced individual differences in earliness within the same ecotype. These observations are shown in graphic form in figure 126, in which the dates of flowering of individuals representing different ecotypes of *Achillea* are plotted. The two plants of *borealis* from

the California coast bloom one month apart both at Stanford and at Mather, and there is about the same difference between the two mid-altitude plants of *lanulosa*.

There are also large earliness differences between the two alpine plants of *lanulosa*, and between the two Alaskan *borealis* plants at both Stanford and Mather. At Timberline, however, these four plants from high altitudes or latitudes flower within the interval of one week. Such modifications are to be expected in environments like Stanford, where these plants are near their margin of survival. They do not thrive well there and behave erratically as to time of flowering, varying considerably from year to year. The alpine *lanulosa* is especially delayed at Stanford, so that it blooms at about the same time as at Mather. This behavior parallels that observed in the mid-altitude ecotypes of *Penstemon procerus* and *Zauschneria californica*.

There is also considerable overlapping in earliness between the ecotypes at Stanford and at Mather as shown in the graph, and it is only at Timberline that they start flowering in the order that would be expected, namely, alpine and Alaskan first, then subalpine, and finally Great Basin. These complex differences indicate that time of flowering in this genus is a character determined by many factors, and consequently is a less dependable indicator of ecotypic difference than in most *Potentillas*.

PRECOCITY AT THE MOUNTAIN STATIONS. A reaction already noted in *Zauschneria* (see fig. 89) is strikingly evident in *Achillea*, in which the length of time elapsing between the emergence of the first new rosette leaves of the season and the appearance of flowers is much shorter at Mather and Timberline than at Stanford. This is shown in table 25. In *A. borealis* the difference is much the greatest for the plants from the California coast, but it is also highly significant in the Alaskan plants. In *A. lanulosa* the mid-Sierran ecotype is affected more than the alpine, but in both, the period of development prior to flowering is much shorter at Mather.

The difference in rate of development at the three stations is doubtless connected with the length of the growing seasons. Most *Achilleas* tend to be evergreen at Stanford, especially *borealis* from the California coast—the group whose rate of development is most accelerated at the mountain stations. Following a brief period of rest

TABLE 25

DAYS ELAPSING BETWEEN EMERGENCE OF FIRST LEAVES AND FIRST FLOWERS IN ACHILLEA
(Averages from three years, 1935 to 1937)

Number and origin of plants	Stanford	Mather	Timberline
<i>Achillea borealis</i> :			
CALIFORNIA COAST:			
1212-2, Half Moon Bay, 5 m.....	193.3	77.0	Immature
1313-3, Pt. Montara, 5 m.....	245.7	82.0	Immature
1313-4, Berkeley, 150 m.....	200.0	73.0
1314-1, Same.....	218.0	71	Immature
Means.....	214.2	75.7
ALASKA COAST:			
2443-1, Seward.....	89.0	42.0	50.5
-2, Same.....	103.0	45.0	51.0
-3, Same.....	86.5	61	56
Means.....	92.8	49.3	52.5
<i>Achillea lanulosa</i> :			
MID-SIERRAN:			
1315-1, Mather, 1425 m.....	193.3	50.0	Immature
-4, Mather, 1400 m.....	226.3	62.3
-5, Mather, 1375 m.....	117.7	59	Immature
Means.....	179.1	57.1
SUBALPINE:			
2459-1, Le Conte Falls, 2165 m.	95.0	54.0	64.0
ALPINE:			
1316-1, Slate Creek, 3260 m.....	148.7	51.0	54.3
-2, Same.....	114	48.0	55.7
Means.....	131.4	49.5	55.0
GREAT BASIN:			
2460-2, Mono Lake, 2100 m.....	128.0	62.5	72.5
<i>Achillea millefolium</i> :			
2442-1, maritime, Denmark, 3 m.....	128.0	68.0	Immature
1808-1, woodland, Denmark, 50 m.....	231.7	84.3	Immature

in the fall, the plants of this subspecies start the season's growth in October or November, with the advent of the winter rains. They continue to increase their rosettes through the spring and are ready to bloom in May. The Alaskan ecotype is nearly dormant for a short period between late November and early January, but then it begins new growth and some time thereafter has flowers. Mid-Sierran plants of *lanulosa* follow a cycle similar to that of Californian *borealis*, but usually start the season's growth two months later, after a period of fall dormancy. The subalpine, alpine, and Great Basin forms of *lanulosa* have a longer rest period at Stanford that extends to January or early February. Here the alpinists flower among the last and sometimes not at all.

At Stanford the Danish ecotypes of *A. millefolium* have unlike responses. The maritime ecotype, which is the only one with a definite period of dormancy, commences growth two months later than the woodland ecotype, but it reaches flower one month earlier, a difference of three months in period of development.

At Mather the picture is very different, for all *Achilleas* are forced into dormancy from October until April or May. They all finish their development at a very rapid rate, although the various ecotypes differ in the time they require. At Timberline, the growth season does not begin until late June or early July, and ends in September. The mid-Sierran and Great Basin forms of *lanulosa* and the Danish maritime form of *millefolium* are evidently much slower in development at Timberline than at Mather, for at Timberline they produce only rosettes in the same period that suffices for flowering at Mather. Even the forms from high altitudes and latitudes use a slightly longer time at Timberline than at Mather, as may be seen from table 25. The growth rate at Mather is more rapid, forms there producing considerably longer stems and leaves in less time.

VIGOR. The number of stems produced at the three stations serves as a suitable index of general vigor. Table 26 shows, for example, how the forms of *A. borealis* from the California coast produce far more stems at Stanford than at Mather, while the proportion is reversed for the Alaskan ecotype. Moreover, the mid-Sierran plants of *lanulosa* produce by far the greatest number of stems at Stanford, while the other ecotypes of this species produce the most at Mather. Likewise there are differences between the Danish forms of *mille-*

folium, the maritime form being most floriferous at Mather, the woodland form at Stanford.

The Alaskan *borealis* and the alpine *lanulosa* have few flowering

TABLE 26
MODIFICATIONS IN ACHILLEA
(Averages from three years, 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS		
	Stan- ford	Math- er	Timber- line	Stan- ford	Math- er	Timber- line
<i>Achillea borealis</i> :						
CALIFORNIA COAST:						
1212-2, Half Moon Bay, 5 m.	95.0	55.0	133.3	55.0	6.0
1313-3, Pt. Montara, 5 m.	70.0	36.0	90.0	30.0	0
1313-4, Berkeley, 150 m.	75.7	42.0	75.0	40.0	0
1314-1, Same.	102.3	44.0	70.0	5.5	0
Means.	85.8	44.3	92.1	32.6	1.5
						Immature
ALASKA COAST:						
2443-1, Seward.	24.0	36.0	12.0	9.3	53.3	4.5
-2, Same.	21.5	40.0	16.5	3.0	35.3	3.5
-3, Same.	16.3	38.0	8.0	1.0	55.0	1.0
Means.	20.6	38.0	12.2	4.4	47.9	3.0
<i>Achillea lanulosa</i> :						
MID-SIERRAN:						
1315-1, Mather, 1425 m.	86.0	59.7	51.7	14.0	1.0
-4, Mather, 1400 m.	74.7	60.7	76.7	14.0	0
-5, Mather, 1375 m.	65.3	62.5	28.0	16.3	1.0
Means.	75.3	61.0	52.1	14.8	0.6
						Immature
SUBALPINE:						
2459-1, Le Conte Falls, 2165 m. .	46.0	41.0	33.0	21.0	33.5	9.0
ALPINE:						
1316-1, Slate Creek, 3260 m.	16.7	26.5	19.7	7.3	13.5	16.3
-2, Same.	12.5	24.0	23.7	3.0	24.0	3.0
Means.	14.6	25.3	21.7	5.2	18.8	9.7
GREAT BASIN:						
2460-2, Mono Lake, 2100 m.	41.3	56.5	30.0	25.3	45.0	12.0
			Immature			
<i>Achillea millefolium</i> :						
2442-1, maritime, Denmark, 3 m. .	28.3	26.5	14.3	25.5	0
1808-1, woodland, Denmark, 50 m.	65.7	66.7	90.0	51.7	3.5
						Immature
PENTAPLOID:						
1317-1, Washington, D.C., 50 m. .	116.0	41.7	136.7	21.0	2.2
						Immature

stems at Stanford, far fewer than can be accounted for by the vigor of their rosettes. The consistent scarcity of flowers on these forms, in marked contrast with the abundant flowering of the others, indicates that their metabolism is differentially affected. The reduced flowering in alpine *Achilleas* at Stanford recalls to mind that alpine and some subalpine *Potentillas* and *Horkelias* likewise show reduced flowering there.

SURVIVAL AND MATURATION. The differences in capacity of the various ecotypes of *Achillea* to survive and to reach maturity at the transplant stations has already been mentioned. Figure 127 gives in graphic form the record of survival and flowering. The failure of California *borealis* and mid-Sierran *lanulosa* to flower or to survive at Timberline is indicated. So is the extended survival of Danish *millefolium* in a non-flowering state. The difficulty with which even the alpine *lanulosa* attains maturity in the Timberline meadow garden is shown by the fact that only the earliest individual, 1316-2, succeeded in producing ripe seed, and that in but one year with a relatively long growing season, 1934. Therefore, *Achillea lanulosa* appears to be a species that has not been able to develop an ecotype truly alpine in character, although it is very abundant in the alpine environment. It must be kept in mind, however, that the transplant garden is in the Timberline meadow, in which no native *Achilleas* grow. They are all on the rocky slopes that have a somewhat longer growing season, as explained on page 87. The slopes apparently furnish the necessary ecological opportunity for this ecotype, which manifestly is at its upper altitudinal limits. The Alaskan *borealis*, which flowers as early as or earlier than alpine *lanulosa*, is less frost-resistant, consequently its inflorescences are frost-killed each year before they are able to mature seed.

All *Achilleas* survive, flower, and mature at Stanford and Mather. The chart, figure 127, shows that three plants of California *borealis* did not flower at Mather during the years between 1926 and 1933. They were grown in a garden half shaded by trees; the shade was sufficient to prevent flowering, for as soon as they were moved to a sunny garden they started to bloom.

Achilleas are plants of sunny habitats. In the water-light gardens at Mather, they seldom flower and are weak in the shade. The alpine *A. lanulosa* is even unable to survive in either of the shade

gardens. The plant of *A. borealis arenicola* from the moist coast, 1313-3, could not grow under either of the dry conditions.

Our transplant data from *Achillea*, as seen from the above tables

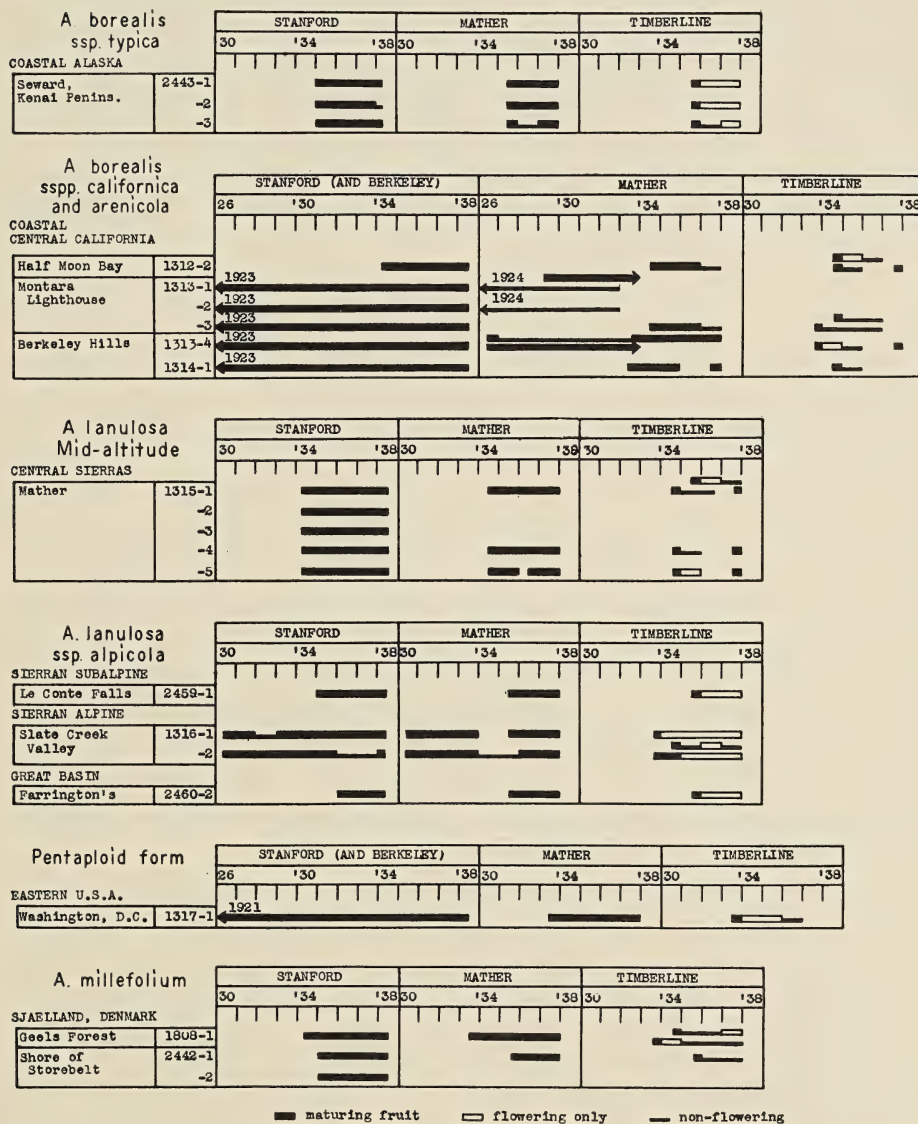


FIG. 127. Record of survival and flowering of clones representing ecotypes and eco-species of *Achillea* at three altitudes. See table 26 for additional data on the individuals represented. The scale indicates years.

and graphs, have been obtained from relatively few individuals. We found it necessary to restrict our studies to so few plants because of the practical difficulty of keeping *Achilleas* free from contamination. The abundant seedlings developing each spring that constantly invade the transplants constitute a serious menace, for they root easily among the rosettes of mature plants and, if not uprooted repeatedly in the early stages, soon develop to a point where they become easily mistaken for part of the rosette of the original plant. Thus, while *Achilleas* have yielded data of much interest, and are in many respects ideal for transplanting, they have this serious drawback that makes them very costly to maintain in pure condition for any great length of time.

CYTOGENETIC STUDIES

While the cytogenetic studies in *Achillea* have been of an exploratory nature only, the evidence obtained has proved of much value in outlining species limits in this complex, as already mentioned.

CYTOLOGY. Chromosomes of the *Achillea millefolium* complex are many and large. In somatic stage they are about four to six microns long and one micron wide. They almost fill the cells in the hexaploids, making the count often slightly uncertain in the center of the plate. Hexaploids also show moderate amounts of irregularities in meiosis. It is therefore possible that in the hexaploids the chromosome number oscillates slightly from plant to plant—a point that will be further investigated. In the following list of those plants whose chromosomes have been studied, most determinations were made on somatic mitoses in roots; but those marked with an asterisk were determined in meiosis also.

A. borealis typica, hexaploid, $n=27$:

2443-1* (*E. Hultén* 7808), Seward, Kenai Peninsula, Alaska.

A. borealis arenicola, hexaploid, $n=27$:

Keck 4765, Clam Beach, north of Eureka, Humboldt Co., California, two plants.

1313-1, -2, and -3*, Montara Point, San Mateo Co.

2458-1*, Asilomar, Monterey Peninsula.

A. borealis californica, hexaploid, $n=27$:

1313-4 and 1314-1, Berkeley Hills, Alameda Co., 50 m.

Hiesey 396-5, southeast of Clayton, Contra Costa Co., 125 m.

Hiesey 396-4, Knights Ferry, Stanislaus Co., 75 m.

Clausen 1714-5, Stanford University, 25 m.

Clausen 1710-3, Seaside, Monterey Co., 5 m., $2n=54 + 6$ fragments; 1710-4, same, $2n=54$.

1820-1*, north of Morro Rock, San Luis Obispo Co., 5 m.

A. lanulosa, mid-Sierran ecotype, tetraploid, $n=18$:

Hiesey 396-1, Groveland, Tuolumne Co., 975 m.

1315-1, -3, and -4, Mather, 1400 m.

1315-11, Cottonwood Meadow, Yosemite Park, 1770 m.

1315-21*, above Aspen Valley, Yosemite Park, 2040 m.

1315-41, Yosemite Creek, Yosemite Park, 2190 m.

A. lanulosa alpicola, tetraploid, $n=18$:

1315-42, Yosemite Creek, 2190 m.

1315-71, Tuolumne Meadows, 2740 m.

2459-1*, Le Conte Falls, Tuolumne River, 2165 m.

1316-1*, -2*, -3, and -4, Slate Creek Valley, Mono Co., 3260 m.

Keck 4839, Mt. Ashland, Jackson Co., Oregon, 2190 m.

A. lanulosa, Great Basin ecotype, tetraploid, $n=18$:

2460-2* and -3*, Farrington's, south of Mono Lake, Mono Co., 2100 m.

It should be remembered that the two plants from Spokane and Seattle determined by Turesson (1938) possibly belong to this subspecies (*typica*); these and his plant from Dunvegan, Alberta, Canada, in the Peace River district, all were tetraploid.

A. millefolium, hexaploid, $n=ca. 27$:

1808-1*, the woodland form from margin of Geels Forest, north of Copenhagen, Denmark.

2442-1*, the maritime form from the Storebelt coast, south of Korsör, Denmark.

Turesson (1938) counted $2n=54$ in a plant from near Uppsala, Sweden.

A. millefolium (?), pentaploid, $2n=ca. 43-46$:

1317-1*, Washington, D. C., quite irregular in meiosis.

GENETIC EVIDENCE. Only one cross has been attempted in *Achillea*. This was between the Danish maritime form of *A. millefolium* and a coastal form of *A. borealis californica* from Berkeley, California, each with 27 pairs of chromosomes. The details follow:

2442-1 (*millefolium*, Danish maritime) \times 1313-4 (*borealis* ssp. *californica*, Berkeley) and reciprocal. A number of heads were emasculated in this cross and the reciprocal, prior to pollination. Also, other heads were not emasculated but were fertilized with pollen from the other species. The plant 2442-1 was also selfed by isolation in a screened cage in the greenhouse. The following results were obtained: (1) None of the sixty emasculated heads fertilized with pollen of the opposite species produced good akenes, indicating complete incompatibility. (2) Of the many heads not emasculated,

but cross-pollinated, seventeen apparently good akenes were harvested, but none germinated. (3) Out of two hundred heads selfed on the Danish maritime plant, only four akenes were obtained, of which two germinated, producing plants like the parent.

The conclusions to be drawn from the results of this experiment are: first, the California and Danish plants are cross-incompatible, and second, both are highly self-incompatible. This evidence, in addition to the morphological differences, is a good indication that the two are distinct species. Because no seeds were obtained after isolation, or after emasculation followed by cross-pollination, a third conclusion follows, that these *Achilleas* are not apomictic. This is of much interest in view of the extreme morphological variation within each species, their polyploid composition, and the evidence of cytological irregularity in some of the forms. Obviously, much remains to be learned concerning the relationships between the forms of the *Achillea millefolium* complex, a group that invites much more thorough study from the taxonomic, geographical, and cytogenetic viewpoints.

IX

THE GENUS ARTEMISIA

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In western North America several sections of the well-known genus *Artemisia* are represented. Some of the species have been included in the varied-environment experiments ever since the American forms were undergoing study and monographing by Hall and Clements (1923). In that paper a very conservative attitude was taken as to species limits, in part as a natural reaction to the unreasonable splitting that the genus had been undergoing at the hands of several workers. At present, with the addition of cytological and crossing data to be considered in forming our judgments, it is evident that a middle course must be followed. In the present investigations we have been concerned particularly with the relatives of *Artemisia vulgaris* L., and the following account deals principally with that complex.

THE ARTEMISIA VULGARIS COMPLEX

Hall and Clements (1923), in their treatment of *Artemisia vulgaris* L., included under that one species and its fifteen subspecies all the American forms, which but seven years previously had been defined as fifty-four species by Rydberg (1916). Our investigations in the group lead us to believe that there are probably about ten distinct ecospecies involved, and apparently a like number of morphologically recognizable subspecies in addition. A taxonomic revision of this complex is in preparation, but here we shall confine our remarks to those species that have been included in our transplant and cytogenetic investigations.

DIFFERENTIATION INTO ECOSPECIES. The *Artemisia vulgaris* complex differs in several respects from any of the cases treated in preceding chapters. There is a certain parallel between the situation in this genus and that in *Achillea*, discussed in chapter VIII, for in each case the European species that has given its name to the collective group is not a member of the west American flora. In *Achillea*, the

European *millefolium* was hexaploid and in that respect comparable with the species of the immediate Pacific Coast from Alaska to California, *A. borealis*. But the two differ morphologically and were shown to be intersterile. There is a tetraploid, *Achillea lanulosa*, to which most of the American material is referable, but no diploid *Achillea* has been discovered.

In *Artemisia*, on the other hand, the European *vulgaris* is diploid, with $n=8$. This chromosome number alone sets it off from all American forms of the complex that have been investigated, because they follow a 9 series of chromosome numbers. One diploid, one tetraploid, and two hexaploid species from North America were included in the transplant investigations, as well as a Swedish form of typical *A. vulgaris*:

Artemisia vulgaris L., Skåne, Sweden, $n=8$

A. Suksdorfii Piper, California coast, $n=9$

A. ludoviciana Nutt., Sierra Nevada to Rocky Mountains, $n=18$

A. Douglasiana Bess., central California, $n=27$

A. Tilesii Ledeb., Alaska, $n=27$

These species are illustrated in figures 128 to 130 by specimens grown under uniform conditions at Stanford.

A striking difference between these species and those of *Achillea* is that the cytological lines are drawn at very different places on the map. Although the ecological pattern is quite similar in the two genera, their cytological patterns are very different. In *Achillea*, the forms from the Pacific to the foothills of the Sierras are hexaploid, but from that point on across the range to the Great Basin and eastward occurs a tetraploid species. In *Artemisia*, along the north coast of California is a diploid species that ventures no more than a few miles inland. To the south of it is a hexaploid species that covers the Coast Ranges and the west side of the Sierras up to about the 1800-m. level. From there to the summit and eastward across the Great Basin and the Rockies grows the tetraploid. Northward the situation likewise is not parallel. In *Achillea*, the hexaploid of the California coast continues to Alaska without interruption. In *Artemisia*, the coastal diploid extends from California to Vancouver Island and dominates the immediate coast between, but farther north it is replaced by a hexaploid species that is on the coast of Alaska, but also spreads inland to the east and south. A fortunate circumstance

in *Artemisia* is that its forms are morphologically rather readily separable, whereas in *Achillea* the structural differences are both obscure and almost masked by intergrades and variation.

The coastal diploid, *Artemisia Suksdorfii* Piper, is shown on the left in figure 128 (1331-1). This has been called *A. vulgaris* ssp. *litoralis* (Suksd.) H. & C. The two specimens next to it, 1318-1 and 1323-1, are referable to *A. Douglasiana* Besser (*A. vulgaris* ssp. *heterophylla* [Nutt.] H. & C.), a hexaploid species. The morphological difference between the two species does not suggest such a great cytological difference. From the illustration it is even difficult to see the key morphological distinction between these species, namely, the difference in the size of the heads. Those of *Suksdorfii* contain only three to seven disk flowers and the yellowish involucre is only 2 mm. broad and nearly glabrous; in *Douglasiana* the heads contain nine to twenty-three disk flowers and the greenish involucre is 2.5 to 3.5 mm. broad and densely tomentose.

Artemisia Suksdorfii is distributed from Vancouver Island to northern Sonoma County, California. From Oregon southward it is confined to the immediate vicinity of the coast, but in Washington it also borders Puget Sound and in British Columbia it is found as far inland as Chilliwack Valley.

Artemisia Douglasiana occurs from south central Washington (Yakima County) southward with increasing frequency through Oregon, almost entirely to the west of the Cascades, through California, where it is most abundant, from the coast to mid-altitudes in the Sierra Nevada and on the floor of the Great Valley, continuing through cismontane California to about latitude 31° N. in Baja California. It crosses the Sierra Nevada through the relatively low Feather River Gap to the vicinity of Lake Tahoe. Also, it appears to be locally spontaneous in northern Idaho.

Representatives of *Artemisia ludoviciana* Nutt. are shown in figure 129. Plant 1324-3 on the left, from near Timberline station, is referable to ***A. ludoviciana* ssp. *incompta*** (Nutt.) Keck comb. nov. (*A. incompta* Nutt., Trans. Amer. Phil. Soc. II, 7:400, 1841). This subspecies has passed frequently under the name *A. vulgaris* ssp. *discolor* (Dougl.) H. & C., which now is thought referable to a more northern species, *A. Michauxiana* Bess. Subspecies *incompta* is the subalpine and alpine form of *ludoviciana*, distinguished by the deeply and twice cut divisions of the lower leaves. Much variation and



FIG. 128. *Artemisia Suksdorfii* (left) and *A. Douglasiana* (center and right), all from California.

Plant 1331-1 is from Trinidad, Humboldt County, at 10 m., 1318-1 from Santa Barbara at 15 m., and 1323-1 from Mather at 1400 m. These specimens are from propagules at Stanford, grown at the coastal stations for about ten years, except 1323-1, which had been there for only three years.

doubtless more than a single ecotype are included in this subspecies, which occurs in the mountains of Montana and Idaho, southward to Utah, Nevada, and California.



FIG. 129. *Artemisia ludoviciana* ssp. *incompta* (left) and ssp. *typica* (the other three).

Plant 1324-3 is from near Timberline station, at 3260 m., 1326-1 from Leevining, Mono County, California, at 1980 m., 1328-1 from Manitou, El Paso County, Colorado, at 1890 m., and 1329-1 from Engelmann Canyon, Pikes Peak. Specimens all from propagules at Stanford, grown at lowland stations for fourteen years except 1324-3 and 1326-1, which had been grown for only seven years.

The remaining plants in figure 129 belong to **A. ludoviciana** ssp. **typica** Keck nom. nov. (*A. ludoviciana* Nutt., Gen. 2:143, 1818). We believe that this form, except in the high mountains, where it is replaced by the preceding subspecies, and in the Northwest, where a larger-headed form intervenes, is the principal one found from the Great Basin to the Mississippi River. Rather locally it extends westward to the eastern flanks of the Cascades and Sierras. It is chiefly confined to the region bounded by the thirty-fifth and the fifty-first parallels, but its exact boundaries fluctuate considerably. The Great Basin form of the subspecies came from Leevining, Mono County, California; the Rocky Mountain plants are from the east flank of Pikes Peak, Colorado. In 1328-1 the leaves are tomentose on both sides, and this form is widely known as *A. gnaphalodes* Nutt.; in 1329-1 the leaves are prominently discolored, almost glabrous above, and densely tomentose beneath, and this matches the type of *A. ludoviciana* Nutt. We consider these forms inseparable into natural subunits, for both sorts occur together intermittently almost throughout the range of the species and obviously intermix. In this instance these characters do not even mark ecotypical differences.

Typical *Artemisia vulgaris* L., originally from Skåne, Sweden, is shown in figure 130 as it grows at Stanford. In the same figure is *A. Tilesii* Ledeb. ssp. *unalaschcensis* (Bess.) Hultén, originally from the Aleutian Islands, Alaska, also shown as it grows at Stanford. This strain is considered by Hultén (1937*b*) to be referable to *A. unalaschensis* Rydb., but we believe that the two names apply to the same unit. Both of these cultures, 3029 and 3030, were started from seed kindly sent by Dr. Göte Turesson from Sweden. The former was collected in the wild, the latter from plants grown by Dr. Eric Hultén from seed he collected on Unalaska of the Aleutians. Both *vulgaris* and *Tilesii* grow well at Stanford, but have been set only recently at the mountain stations.

Artemisia vulgaris is native almost throughout Eurasia and has been introduced extensively into the eastern United States, a parallel to the situation in *Achillea millefolium*. A total of twenty plants of the south Swedish *Artemisia vulgaris* was grown in the Stanford garden. They developed into vigorous plants with stems at least as long as in northern Europe. It was very surprising, however, that at Stanford most of the plants were spreading or almost depressed, whereas in Europe the species is erect to ascending-erect. One

almost erect plant was 115 cm. tall by 130 cm. wide, whereas an almost prostrate plant was 40 cm. in height and 170 cm. wide. They flower well at Stanford.



FIG. 130. Left: an F_1 hybrid between *Artemisia Douglasiana* and *A. ludoviciana typica* (3033-2).

Right: *Artemisia vulgaris* (upper, 3029) and *A. Tilesii* ssp. *unalaschcensis* (lower, 3030) with leaf variations. Both specimens were raised from seed and grown at Stanford. See text.

Artemisia Tilesii ssp. *unalaschcensis* is found from the Aleutians and the south coast of Alaska eastward to Northwest Territory and southward to the mountains of Washington and western Montana. The species itself occurs from Hudson Bay westward across central

and northern Alaska and Siberia to Nova Zembla and arctic Russia. The twenty plants of *A. Tilesii unalaschcensis* in the Stanford garden are variable in cut and pubescence of basal leaves, some of which are shown in figure 130. The plants flower freely and are vigorous. The stems are ascending-erect, producing plants varying between 40 and 80 cm. in height, and between 70 and 120 cm. in width. The many dark green and very large rosette leaves, that remain alive all winter at Stanford, give this species a characteristic appearance; large leaves also subtend the inflorescence.

Shown also in figure 130 is a pentaploid hybrid (3033-2, $2n=45$) obtained as F_1 of the cross *A. Douglasiana* \times *ludoviciana*. The *Douglasiana* parent, which is hexaploid, came from Santa Barbara, California, and is pictured in figure 128 (1318-1); the *ludoviciana* parent, which is tetraploid, came from Manitou, Colorado, and is shown in figure 129 (1328-1). The hybrid is intermediate between its parents in most characters. It is sterile and is one of two that were obtained from a controlled mutual pollination.

TRANSPLANT RESULTS

The principal reactions and modifications of members of *Artemisia* subsection *Vulgares* in the transplant experiments are summed up in table 27 and figures 131 to 134.

SURVIVAL, VIGOR, AND HEIGHT. Coastal forms of *A. Douglasiana* grow very vigorously at Stanford and Berkeley, and usually succeed at Mather. A prominent exception is the plant 1318-1 (see fig. 128), from Santa Barbara, near sea level. Well-established clone members of this plant set in gardens at Mather invariably are winter-killed the first year after transplanting, while propagules of another plant of this species, 1319-1, originally from Pismo Beach some miles north of Santa Barbara and morphologically quite similar to the Santa Barbara plant, develop vigorously at this station. This difference is evident in the survival graph, figure 131. The two individuals show only small morphological differences, but there must be important physiological dissimilarities within them. Other plants originally from various points along the coast north of Santa Barbara also thrive at Mather.

Appreciable individual differences are evident within the species, subspecies, or even the local population, as shown in table 27 by the

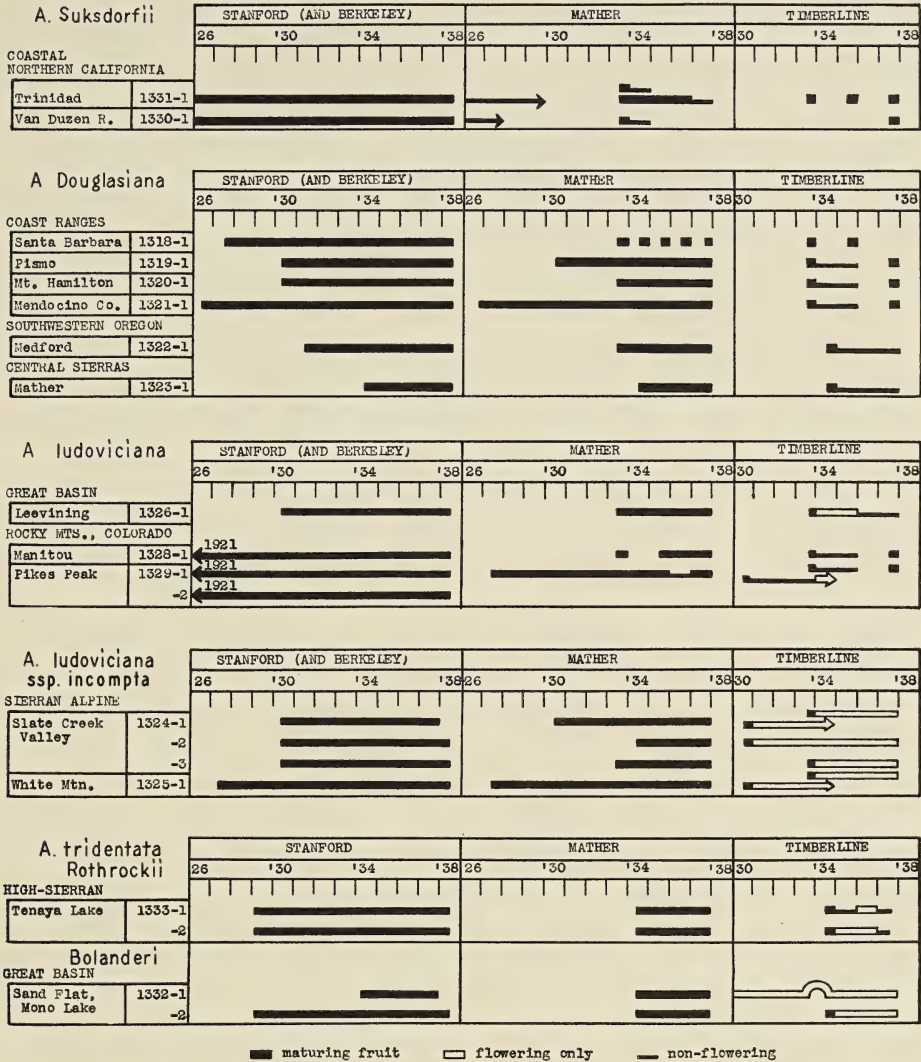


FIG. 131. Record of survival and flowering of clones of plants representing ecotypes and ecospecies of *Artemisia* at three transplant stations. See tables 27 and 28 for further data on the individuals represented. The scale indicates years.

tabulations for length and number of stems, and for earliness. In *A. Douglasiana* at Stanford, for example, there is considerable difference between the individuals in height. Plant 1321-1 is by far the tallest at Stanford, but is surpassed by others at Mather. As shown by the means, this species, which is most abundant in the lowlands, grows taller at Stanford than at Mather, but the number of stems

TABLE 27
MODIFICATION IN ARTEMISIA SUBSECTION VULGARES
(Averages from four years, 1934 to 1937)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
<i>Artemisia Suksdorfii</i> :									
1330-1, Van Duzen River, Humboldt Co., Calif., 50 m.....	165.7	125.0	May 16.5
1331-1, Trinidad, Humboldt Co., Calif., 10 m.....	150.3	(35)	(16)	90.0	(15)	May 20.0
Means.....	158.0	107.5	May 18.3
<i>Artemisia Douglasiana</i> :									
COAST RANGE:									
1318-1, Santa Barbara, 15 m.....	147.5	100	67.5	(Jul. 29.3)
1319-1, Pismo Hills, 30 m.....	158.8	117.0	(28.0)	80.0	61.7	11.0	Jun. 29.0	Aug. 18.3
1320-1, Mt. Hamilton, 490 m.....	133.8	123.0	(34.0)	65.0	85.0	21.5	Jun. 15.3	Aug. 9.3
1321-1, Mendocino Co.....	175.0	116.5	(28.5)	73.3	43.3	16.0	Jul. 2.3	Aug. 10.0
1322-1, Medford, Ore., 415 m.....	123.8	108.8	(31.3)	60.0	83.3	30.0	Jun. 13.0	Aug. 12.5
Means.....	147.8	113.1	(30.5)	69.2	68.3	19.6	Jun. 22.4	Aug. 12.5
SIERRA NEVADA:									
1323-1, Mather, 1425 m.....	126.3	111.0	(19.3)	76.7	35.0	13.3	Jul. 11.3	Aug. 21.0
<i>Artemisia ludoviciana incompta</i> :									
1324-1, Slate Creek Valley, Mono Co., 3260 m.....	72.0	87.3	49.3	51.7	136.7	38.3	Jul. 2.5	Jul. 13.8	Sep. 8.0
-2, Same.....	81.8	108.5	24.0	61.7	83.3	28.3	Jun. 22.0	Jul. 1.7	Sep. 4.3
-3, Same.....	76.5	100.0	31.0	53.3	98.3	22.7	Jun. 21.0	Jul. 2.5	Sep. 8.0
1325-1, White Mt., Tuolumne Co., 3200 m.....	53.8	53.0	17.0	40.0	78.3	15.0	Jun. 13.7	Jul. 3.0	Sep. 24.3
Means.....	71.0	87.2	30.3	51.7	99.2	26.1	Jun. 22.3	Jul. 5.3	Sep. 11.2
<i>Artemisia ludoviciana typica</i> :									
CALIFORNIA:									
1326-1, Leevining, 1980 m.....	115.7	107.8	(42.5)	80.0	105.0	23.3	May 17.7	Jul. 12.8	(Sep. 30)
COLORADO:									
1328-1, Manitou, 1890 m.....	112.5	93.5	(20.0)	72.5	42.5	21.0	Jul. 27.7	Aug. 19.0
1329-1, Engelmann Canyon, Pikes Peak.....	74.0	71.3	(24.0)	48.3	28.0	15.0	Jul. 16.0	Aug. 9.7
Means.....	100.7	90.9	(28.8)	66.9	58.5	19.8	Jun. 30.1	Aug. 3.5

() Not included in means, usually because immature.

remains essentially the same at the two stations. It will be recalled that *Achillea borealis* from the Coast Ranges and *A. lanulosa* from Sierran mid-altitudes show approximately the same reactions as the corresponding forms of *Artemisia Douglasiana*.

The individual of *A. Douglasiana* from the Sierra Nevada, 1323-1, is quite comparable with the Coast Range forms in its reactions, but in the Mather garden, in its native habitat, it produces only about half the average number of stems that the coastal forms produce. Also, as table 27 shows, it blooms very late, and at Timberline it succeeds no better than the coastal forms. These observations probably correlate with the fact that the Mather plant lives near the altitudinal upper limit for the species and does not appear to belong to a different ecotype from the one in the Coast Ranges.

Plants of *Douglasiana* are unsuccessful at Timberline. They may survive a few years, meanwhile producing half-grown stems during the short season, but never any flower buds. This is indicated in figure 131 and table 27.

The diploid and strictly coastal *Artemisia Suksdorfii* is definitely a poor survivor at Mather. In this respect it is parallel to the diploid and likewise strictly coastal *Zauschneria cana*. In six attempts the average survival was only nineteen months. The longest survivals were in moist shade and in a moist plot in the old gardens, where the plants were half shaded by trees, but where they did not flower (see fig. 131). At Mather, its stems become much more reduced in length than those of *A. Douglasiana* (fig. 133 and table 27). Mather is therefore definitely at the upper limit for survival of *Artemisia Suksdorfii*. It is of interest that a local difference in habitat, such as increased shade and moisture, will produce a significant response in an individual living in a climate on the threshold for its survival. At Timberline, individuals of this species die promptly the first season.

Very notable modifications are induced in the alpine *Artemisia ludoviciana incompta* when it is planted at the three stations. Of special interest, as shown in table 27, is the observation that it increases in height over 230 per cent at Stanford as compared with Timberline, and that it becomes nearly three times as tall at Mather as at Timberline. The number of flowering stems is just as remarkably increased at the two lower stations, at each of which it thrives for many years. From the survival graph (fig. 131) we see that it

flowers year after year at Timberline without producing ripe fruit. Although on the warmer south slopes this form ascends to 3250 m. near Timberline station, it seems to be pioneering at these high levels. At present it appears able to reproduce itself by seedlings only in very exceptional years in the Timberline garden. However, its strong vegetative system, dependent upon extensive underground rootstocks, makes the production of ripe seeds even every few years quite immaterial to its survival in high alpine conditions.

It is of interest that one plant of the alpine population, 1324-1, differs from the others of this tetraploid species in being hexaploid ($2n=ca. 54$). Since it otherwise does not differ appreciably from the other plants of its population, it seems plausible to suppose that it arose as an autopolyploid from the tetraploid *ludoviciana incompta* through the union of a diploid and a haploid gamete. Occasional production of diploid gametes is to be expected in climates so extreme as the alpine. Table 27 shows that at Stanford and Mather the hexaploid plant tends to be a little later and to have shorter stems than the others. This is confirmed by its behavior in the water-light gardens, where the hexaploid is consistently later than the tetraploids. At Timberline, however, the hexaploid is as early as the diploids, and there also it has consistently longer and more numerous stems than other plants of the alpine population. Therefore, what might appear as a slight disadvantage at the other stations does not handicap it in its native environment.

The reactions of another alpine individual at the three stations are shown in figure 132. The striking increase in stem length at Stanford and Mather as compared with that at Timberline is evident. The reduction in size of the plant when taken from its original habitat to the Timberline interstation garden is also interesting. Like the *Achilleas* mentioned in the preceding chapter, these forms do not favor the alpine meadow floors, but are found on the rocky talus slopes, where it is probably somewhat warmer. Therefore, the garden at 3050 m. is apparently a less favorable locality for the growth of this plant than its native habitat at 3200 m.

Since differences in stem length indicate the extent of modifications in *Artemisia* at the transplant stations, these are summarized in the graph, figure 133. There is a very marked decrease in length of *Suksdorfii* at Mather, and a smaller decrease in length of Coast Range *Douglasiana* at the same station. Even the Sierran *Douglasiana* is

slightly smaller in its native environment than at Stanford, and *ludoviciana typica* from the Great Basin and Colorado follows the same pattern. The only group that produces longer stems at Mather than at Stanford is the alpine *ludoviciana incompta*. This is also the only form that is able to complete the growth of its stems at Timberline, although it very seldom produces mature seed there.

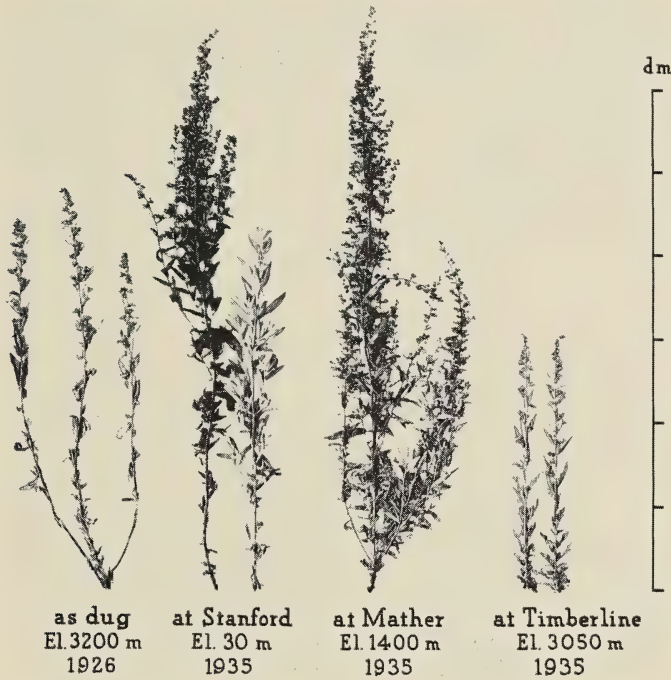


FIG. 132. Modifications in a clone of *Artemisia ludoviciana* ssp. *incompta* at three altitudes.

This plant, 1325-1, was dug September 12, 1926, on White Mountain, Yosemite Park, at 3200 m. The Stanford propagule was transferred in 1929 from Berkeley; the one at Mather was set in 1927; and the division at Timberline (taken from the one at Mather) in 1933. Specimens taken in the years indicated.

EARLINESS. Differences in time of flowering are among the most interesting and impressive reactions in *Artemisia*. They are shown both in table 27 and in figure 134, where three comparisons stand out. At Stanford the mean flowering time of *A. Douglasiana* from the Coast Ranges and of *A. ludoviciana incompta* is the same, but at Mather the alpine species is more than five weeks earlier than the lowland one. At Timberline no comparison is possible because of the failure of *Douglasiana* to mature, but it is significant that the

alpine is the only form in the whole group that develops with sufficient rapidity to flower there consistently.

Another interesting fact is that at both Stanford and Mather the Santa Barbara plant of *Artemisia Douglasiana*, 1318-1, flowers more than one month later than the other Coast Range plants. Like *A.*

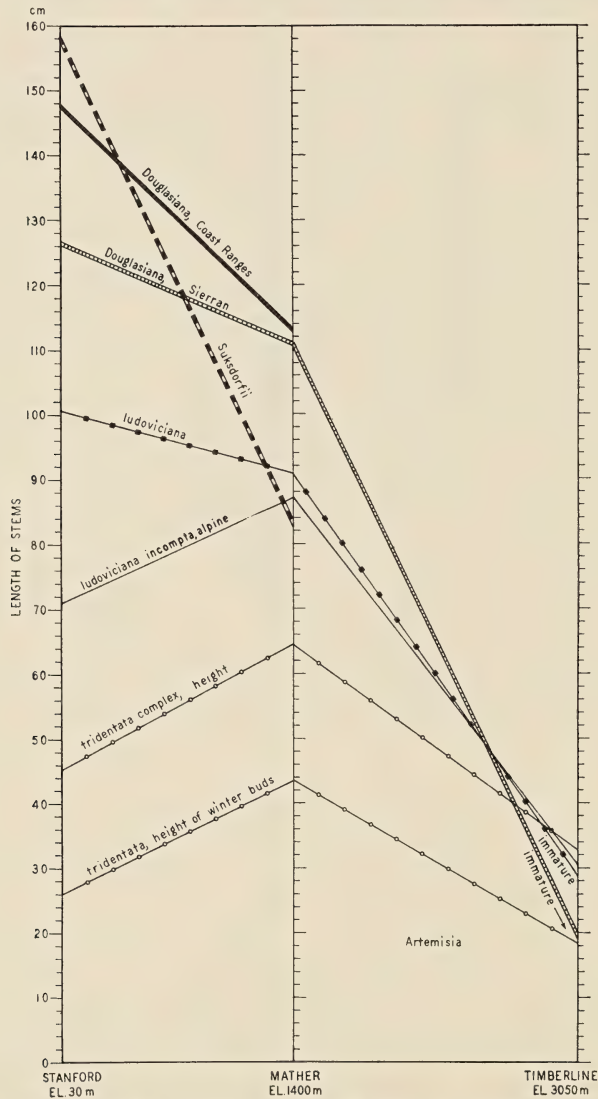


FIG. 133. Modifications at three altitudes in length of stems in clones representing ecotypes and ecospecies of *Artemisia*.

Graphed data averaged from the years 1934 to 1937, for the plants listed in tables 27 and 28.

Suksdorfii, it does not survive at Mather, but is two to three months later at Stanford and Mather than this early-flowering diploid.

The third striking difference in time of flowering is within *A. ludoviciana typica*. As shown in table 27, 1326-1, from Leevining, is

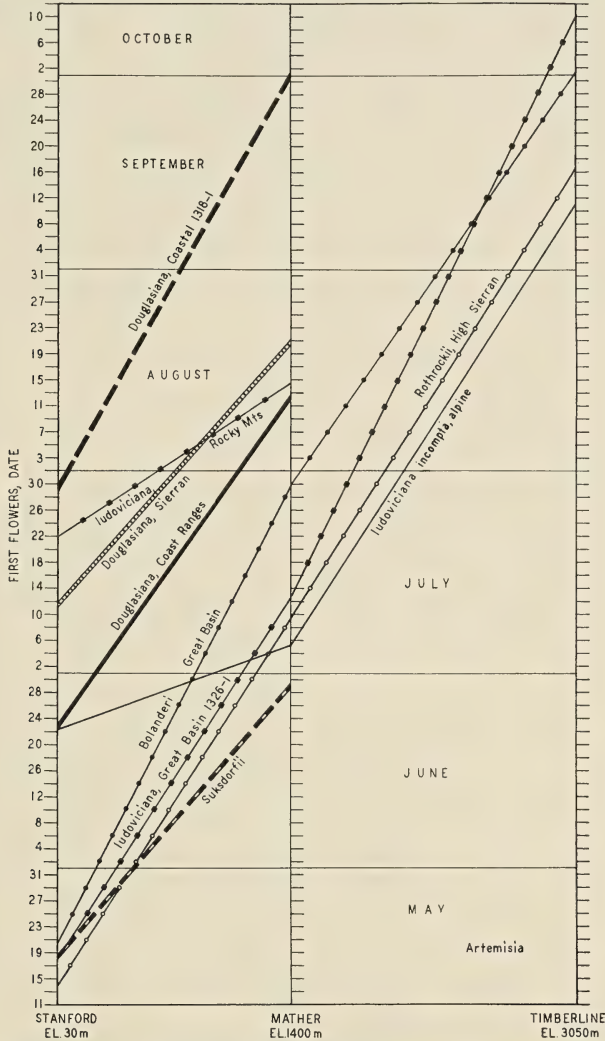


FIG. 134. Modifications at three altitudes in earliness in clones representing ecotypes and ecospecies of *Artemisia*. Data from the same sources as in figure 133.

exceedingly early as compared with 1328-1 and 1329-1, from Colorado—two months earlier at Stanford and one month at Mather. From these isolated observations one might infer that there were more significant distinctions between the Colorado and California materials

than the taxonomic story disclosed. However, another form of this subspecies from Upper Fern Valley, San Jacinto Mountains, California, blooms at Stanford at the same time as the Colorado plants. While a much larger sampling might disclose ecotypical differences with which distinctive morphological characters could be correlated, our present information is inconclusive.

OTHER DIFFERENCES. Almost all the forms of the *Artemisia vulgaris* complex have a period of dormancy at all three stations and reproduce new stems from the ground in the spring. The only exceptions to that rule are the plants of *Artemisia Suksdorfii* and the Santa Barbara plant of *A. Douglasiana*, 1318-1, which at Stanford are almost suffrutescent. They are quite active there in December and January, growing new side branches from the woody stems, but frosts usually kill their old stems before spring and they, too, are forced to start again from the ground. These plants appear to be more tender than the others, and their young shoots are often frost-killed in the spring at Mather.

Alpine plants of *Artemisia ludoviciana* and even the mid-Sierran plants of *Douglasiana* are attacked by rust at Stanford almost every summer, but *Artemisia Douglasiana* from the Coast Ranges is rarely infected. The Great Basin form of *ludoviciana* is intermediate in this respect, whereas the Colorado plants are resistant. We have found that plants native in the mountains, when brought to the lowland station, commonly suffer from diseases that do not attack them in their home nor harm the races native in the lowlands. One possible explanation is that the mountain plants are genetically susceptible, but are not attacked in their home because of unfavorable conditions for the parasite; another is that their usually weakened condition in the lowland environment makes them susceptible.

REACTIONS IN THE WATER-LIGHT GARDENS. Six California plants of the *Artemisia vulgaris* complex were grown in the water-light gardens at Mather. These were:

Artemisia Douglasiana: 1319-1 from Pismo and 1323-1 from Mather

A. ludoviciana incompta: 1324-1 and -3 from Slate Creek Valley and 1325-1 from the adjacent White Mountain, Yosemite Park

A. ludoviciana typica: 1326-1 from Leevining, Mono County

Excepting the Mather plant, which did not flower in dry shade, these plants flowered annually in all four environments. They all

produced slightly longer stems in the shade gardens and usually a larger number of stems in the sun gardens, especially in the dry sun. This trend was very noticeable in all plants of *ludoviciana*, and especially in 1326-1 from the Great Basin. This is quite in character with the habitats usually occupied by these plants. In all the forms, leaves were much thinner in shade than in sun. The *Artemisias* did not show the usual delay of flowering in the moist shade gardens observed in all other species.

A seventh plant, *Artemisia Suksdorfii* 1331-1, from the mild and moist coast of Trinidad, Humboldt County, died in moist sun and dry shade, survived but did not flower in the somewhat protected dry sun garden, and flowered only in moist shade.

CYTOGENETIC STUDIES

CYTOLOGY. The chromosomes of the species of the *Artemisia vulgaris* complex are approximately of the same large size as those of the *Achilleas*. They offer similar technical difficulties in their investigation. A regular polyploid series is formed by the west American species of *Artemisia*, in which the diploid is not missing as in *Achillea*. The determinations were made in somatic mitoses in roots, except for those plants marked with an asterisk, which were determined in meiosis:

Artemisia Suksdorfii, diploid, $n=9$:

1330-1*, Van Duzen River near Carlotta, Humboldt Co.

1331-1*, Trinidad, Humboldt Co.

A. ludoviciana typica, tetraploid, $n=18$:

1326-1, Leevining, Mono Co., 1980 m.

886-B, Fern Valley, San Jacinto Mts., 1525 m.

1328-1*, Manitou, Colorado, 1890 m.

1329-1, Engelmann Canyon, Pikes Peak, Colorado.

A. ludoviciana incompta, tetraploid, $n=18$:

1324-3, Slate Creek Valley, Mono Co., 3260 m.

1325-1, White Mt., Yosemite Park, 3200 m.

Hexaploid form of *incompta*, $2n=ca. 54$:

1324-1, Slate Creek Valley, 3260 m.

A. Douglasiana, hexaploid, $n=ca. 27$:

1318-1, Santa Barbara, 15 m.

1319-1, Pismo Hills, San Luis Obispo Co., 30 m.

1320-3, Santa Cruz Mts., above Los Gatos, 450 m.

1320-1 and -2, Halls Valley, Mt. Hamilton, Santa Clara Co., 490 m.

1322-1, Medford, Josephine Co., Oregon, 415 m.

332-4 and 501-A, Mather, Tuolumne Co., 1400 m.

A. Tilesii unalaschcensis, hexaploid, $n=27$:

3030*, Unalaska, Aleutian Islands.

A. vulgaris, diploid, $n=8$:

3029*, Skåne, southern Sweden.

It is surprising that *A. vulgaris* has 8 pairs of chromosomes when the American species follow a 9 series. Weinedel-Liebau (1928) counted 9 pairs of chromosomes in meiosis (diaphase) of this species. However, figure 5-2 of that paper does not appear very convincing as to whether the chromosome number is actually 8 or 9. No possibility of mistake appears possible in the present determination, which is based on first and second metaphase. However, the determination was made on a single hermaphroditic plant of a gynodioecious race. Our plant came from within the area of the type of the species.

The hexaploid *ludoviciana incompta* and its possible origin were discussed on page 336. Meiosis of this plant has not yet been investigated. It has no connection with or resemblance to the hexaploid species, *A. Douglasiana*.

POSSIBLE ORIGIN OF ARTEMISIA DOUGLASIANA. The three California species of the *vulgaris* complex, shown in figures 128 and 129, are of special interest because of their cytological, morphological, and geographical differentiation. On the immediate west coast is a diploid species, *A. Suksdorfii*, a tall form of restricted distribution, that does not penetrate inland, and that has been shown to be unfitted for higher elevations.

In the drier regions of the United States, from the Great Plains westward across the Rocky Mountains and the Great Basin to the Sierra Nevada and Cascade Range, occurs *A. ludoviciana*. This is a tetraploid species smaller in stature than *Suksdorfii*. Within this large territory it has developed great diversity, and one ecotype has been able to ascend to alpine elevations. Although this species does not populate cismontane California, it seems to have penetrated through the Columbia River gap to northwestern Oregon, where it is found approximate to *Suksdorfii*.

In the geographically and climatically intermediate zone from mid-elevations in the Sierra Nevada to the California Coast Ranges, in which neither of the preceding species occurs, one finds *A. Douglasi-*

ana. This species resembles *Suksdorfii* in stature and herbage, but in its inflorescence and heads it is more like *ludoviciana*. It is also intermediate in its reactions at the transplant stations. Whereas *ludoviciana* survives at all three stations and *Suksdorfii* survives only at the lowest, *Douglasiana* thrives at both of the lower stations. It is also intermediate in regard to modification of stem length at Mather, and in its reactions in the water-light gardens.

Adding to these points the fact that *Suksdorfii* is a diploid species and *ludoviciana* a tetraploid, and that *Douglasiana* has a chromosome number that is the sum of those of the other two species, it becomes tempting to suggest that where *ludoviciana* met *Suksdorfii*—probably somewhere in the Columbia River valley near the Pacific—a new hexaploid species, *Douglasiana*, arose, which was fitted to populate the unoccupied areas farther south.

BREEDING WORK. The *Artemisias* are wind-pollinated and rather highly self-incompatible plants, although a few selfed offspring may be obtained. This was shown in protecting the inflorescences with parchment bags before flowers opened and harvesting the akenes produced under the bag. From the plant 1318-1, *Douglasiana* from Santa Barbara, seven selfed offspring were thus obtained, and from 1328-1, *ludoviciana typica* from Manitou, Colorado, ten selfed plants were grown. In both cases, the offspring resembled the parents, except that their vigor was much reduced.

The cross between *A. Suksdorfii* and *ludoviciana* has not yet been attempted, but a pentaploid hybrid between *Douglasiana* and *ludoviciana* was produced (fig. 130). The details are given below:

A. Douglasiana, 1318-1, Santa Barbara, $n=27 \times A. ludoviciana typica$, 1328-1, Manitou, $n=18$:

No emasculation was employed, but inflorescences were bagged before the opening of flowers, and pollen was introduced later. Thirty seedlings were obtained, most of which were selfed *Douglasiana* with discolored and wide leaves. However, two F_1 hybrids were obtained; they grew more slowly and had narrower leaves, white-tomentose on both sides. In a preliminary test these two hybrids appear sterile, not only when isolated from all others and mutually pollinated, but also when open pollinated in a plot where other *Artemisias* were growing, including the parents.

The chromosomes in the pentaploid hybrid, *A. Douglasiana* \times *ludoviciana*, conjugate fairly readily. Seldom more than 7 univalents can be found and sometimes no more than 3. A *Drosera* type of con-

jugation would give 18 pairs and 9 univalents. The extra pairs should be expected to indicate autosyndesis among chromosomes of the extra set of 9 in *Douglasiana*. The univalents do not scatter over the spindle but arrange themselves along the equatorial margin of the chromosomal plate of bivalents. Occasional trivalents are observed. This behavior indicates a high degree of homology between chromosomes, which suggests that *Douglasiana* and *ludoviciana* are members of one cenospecies. It is to be expected, therefore, that offspring of this hybrid may occasionally be obtained. Possibly all members of subsection *Vulgares* constitute one cenospecies, with *Artemisia vulgaris* L. as the name-giving type species.

Many interesting problems in this circumpolar complex await a much more detailed investigation. The present studies have only opened up the problem and point the way forward. However, even limited experimental investigations like the present one give hints as to the nature and origin of some of the species.

THE ARTEMISIA TRIDENTATA COMPLEX

The sagebrush is one of the most common and widely distributed shrubs in western North America, covering extensive areas in the semiarid plains and plateaus of the western United States. It includes less variety than the *Artemisia vulgaris* complex, although a group of several closely related species make up the sagebrush associations of the ecologist. From cytological and morphological data it appears that the material which Hall and Clements (1923) included in the well-known *Artemisia tridentata* Nutt. is separable into several ecospecies, with widely differing chromosome numbers and occupying rather well-defined geographical areas.

RECIPROCAL TRANSPLANTATIONS. One of the early reciprocal transplant experiments involved two of these, *A. Bolanderi* Gray, of the Great Basin and the eastern slope of the Sierra Nevada, which is diploid, $n=9$, and *A. Rothrockii* Gray, an inhabitant of high altitudes along the Sierran crest, which is octoploid, $n=ca. 36$. A series of individuals of the latter species was transplanted by Hall from Tuolumne Meadows, on the transplant station transect at 2740 m. elevation, to a desert habitat at Sand Flat, south of Mono Lake, at 2050 m. elevation. The plants were set in holes from which individuals of *Bolanderi* had been removed, and the latter, in turn, were

then planted at Tuolumne Meadows in the identical locations from which the plants of *Rothrockii* were dug.

Records taken seven years later show that the essential differences between the two species remained unchanged after this exact exchange of environments (fig. 135). *Artemisia Bolanderi* is distinguished by its narrowly linear, white-tomentose leaves in contrast with the broader, cuneate, gray-green leaves of *Rothrockii*. Although the leaves of *Bolanderi* tended to become slightly broader and less pubescent at Tuolumne Meadows than in its native habitat, and, conversely, the leaves of *Rothrockii* became slightly smaller at Sand Flat, neither species became anything like the other as a result of the experiment.

Of the five original plants of *Artemisia Rothrockii* taken from Tuolumne Meadows to the desert in 1922, one still survived in 1927, but had died in 1929. On the other hand, the transplants of *Bolanderi* from Sand Flat succeeded well at Tuolumne Meadows, even though the latter location has a much shorter growing season. Indeed, two of these original individuals are still in the cultures with propagules distributed to all three stations and thriving.

SURVIVAL AND EARLINESS. Two clones of *A. Rothrockii* from Tenaya Lake have been growing at Stanford for ten years and at Mather for five years, but at Timberline they persisted for three years only (fig. 131). *Artemisia Bolanderi*, on the other hand, survives indefinitely at Timberline. One clone has been there for five years and another for ten years with the exception of one winter, when it was taken to Stanford for propagation (indicated in fig. 131 by a curve in the line). At Stanford, one clone has survived for ten years, but another died after a little more than three years. However, *A. Bolanderi* is severely attacked by rust every summer at Stanford, whereas *Rothrockii* is resistant.

Other reactions of these species are indicated in figures 133 and 134 and in table 28. From the table it is apparent that both species attain their best development at Mather. *Artemisia Bolanderi* succeeds almost as well at Timberline as it does at Stanford as measured by height and number of branches produced, but *Rothrockii* is definitely less successful at Timberline than at Stanford. This is particularly notable because *Rothrockii* is native at subalpine and alpine elevations in the Sierras and might be expected to succeed much better at



FIG. 135. Stability of the characters of *Artemisia Bolanderi* ($n=9$) when transplanted into the habitat of *A. Rothrockii* ($n=36$).

The *Bolanderi* plant was dug August 7, 1922, at Sand Flat, near Mono Lake, California, at 2050 m., while *Rothrockii* was taken the same year from Tuolumne Meadows, at 2650 m. The specimen in the center shows the appearance of *Bolanderi* after seven years in the climatically very different habitat of *Rothrockii*.

TABLE 28
MODIFICATIONS IN GENOSPECIES ARTEMISIA TRIDENTATA
(Averages from three years, 1935 to 1937)

NUMBER AND ORIGIN OF PLANTS	HEIGHT (CM.)			NUMBER OF BRANCHES			DATE OF FIRST FLOWERS		
	Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
<i>Artemisia Bolanderi</i> :									
1332-1, Sand Flat, Mono Lake, 2050 m.	38.3	64.3	39.0	27.3	63.3	31.0	May 17.3	Jul. 29.7	(Oct. 1.0)
-3, Same.....	34.7	60.7	35.7	40.0	58.3	20.0	May 22.5	Jul. 29.3	(Oct. 1.0)
Means.....	36.5	62.5	37.4	33.7	60.8	25.5	May 19.9	Jul. 29.5	(Oct. 1.0)
<i>Artemisia Rothrockii</i> :									
1333-1, Tenaya Lake, Yosemite Park, 2500 m.....	46.0	60.7	25.0	39.7	102.7	7.0	May 16.7	Jul. 7.7	Sep. 17.0
-2, Same.....	62.7	72.3	30.0	80.0	83.3	6.5	May 11.0	Jul. 11.3	Sep. 16.5
Means.....	54.4	66.6	27.5	59.9	93.0	6.8	May 13.9	Jul. 9.5	Sep. 16.8

() Immature.

Timberline. The Tenaya Lake race of this octoploid species is evidently adapted to a different range of environments than the Sand Flat race of the diploid *A. Bolanderi*.

The octoploid *A. Rothrockii* is earlier in all environments than the diploid *Bolanderi*. This is at variance with a generally accepted rule concerning earliness of related polyploids. At Mather the difference is almost three weeks. At Timberline *Rothrockii* is often in flower at the time the last notes of the season are taken, while *Bolanderi* is in bud. Both species show a marked frost resistance, so that in falls of ordinary severity *Bolanderi* should be able to open its flowers under conditions in which this would be impossible for such herbaceous forms as the *Potentillas*. An arbitrary date of October 1 was therefore set as the flowering date of this species. With such a late start, it is of course impossible for either one to ripen akenes at Timberline in any year. Although the races that we have tried of both species are unfitted to the Timberline environment because of their late flowering, there is an alpine race of *Rothrockii* native on the rocky slopes above the Timberline transplant gardens.

MODIFICATION IN LIFE FORM. These two species are the only true shrubs from which a complete transplant record has been obtained. It will be recalled that the suffrutescent *Zauschneria cana* and *Z. californica* ssp. *angustifolia* died at Timberline and survived very poorly even at Mather. Since the shrubby *Artemisias* live in the three very different climates, it is of interest to study their behavior. Following Raunkiaer's classification (1934, II) as to life form, both are nanophanerophytes in their native habitats, for on most shrubs some winter buds are more than 30 cm. above ground. The upper part of the plant dies during the winter, as may be seen in the graphs showing the height of plants during the summer and the height of buds surviving the winter (fig. 133). While they remain as nanophanerophytes at Mather, they would be classed as chamaephytes at both Stanford and Timberline.

At Stanford the height of the surviving buds remained the same after the first year. At Mather, on the contrary, although the plants obtained their full height the first year, the height of the surviving buds increased annually during the three-year period they were measured. This may be seen from the following tabulation:

Plant number and origin	Height above ground of surviving buds (cm.)		
	1935	at Mather 1936	1937
<i>Artemisia Bolanderi</i> :			
1332-1, Sand Flat, Mono Lake.....	25	40	45
-2, Same.....	29	37	47
<i>Artemisia Rothrockii</i> :			
1333-1, Tenaya Lake.....	20	28	46
-2, Same.....	22	50	55

Because the total height of the plants remained constant each summer, the increase in height of winter buds is presumably connected with the hardening of the wood.

MODIFICATIONS IN THE WATER-LIGHT GARDENS. Only *A. Bolanderi*, 1332-3, was tested in this series of gardens. It thrived and flowered equally well in dry and moist sun gardens, but it did not flower in moist shade, and died in the dry shade. These observations are of interest in connection with the fact that the species grows in dry, sunny places.

CYTOLOGY. The chromosome numbers of one plant of each species were determined. These were:

- 1332-3, *A. Bolanderi*, Sand Flat, Mono Lake, 2050 m., diploid, $n=9$. Determined in gametic division in pollen.
- 1333-1, *A. Rothrockii*, Tenaya Lake, 2500 m., octoploid, $n=ca. 36$. Determined in first metaphase of meiosis in pollen mother cells.

Both species have chromosomes of a size comparable with those in the *Artemisia vulgaris* complex. The large chromosomes crowd the pollen mother cells of *A. Rothrockii*, leaving little space between chromosomes and for the cytoplasm outside the nucleus. This condition makes an exact count in this species very difficult, although the divisions take place with great regularity.

Diettert (1939) determined the chromosome number of one of the more northern forms of the *Artemisia tridentata* complex. He stated (p. 7) that the diploid number was 18, but his figure 20 of first metaphase of a pollen mother cell shows that it is the haploid number which is 18. Accordingly, it was a tetraploid species of the *tridentata* complex. Unfortunately, Diettert did not indicate either the systematic unit from which his figure 20 was derived, or the geographical locality of the plant.

It is rather remarkable to find such great differences in chromosome number within what Hall and Clements (1923) considered one species, *Artemisia tridentata*. It was especially surprising to find the greatest differences between two species from Tenaya Lake and Mono Lake, no more than thirty miles (50 km.) apart, although separated by a high mountain crest, and to find the presumably primitive diploid species in a typical desert basin. However, the two habitats are climatically very different. It is to be expected that other links in the polyploid series may be discovered in Mono County, for four of Hall and Clements' subspecies converge there.

With morphologically very distinct diploid, tetraploid, and octoploid forms already discovered, it appears that *Artemisia tridentata* is composed of an assemblage of heteroploid ecospecies adapted to different kinds of environment, although all are of the arid type. This opens up the possibility of making new discoveries through a cyto-taxonomic survey of one of the most characteristic plants of the North American arid regions.

X

MISCELLANEOUS SPECIES

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The previous chapters have dealt with studies in groups of complex composition. These were selected because of their suitability for experimental investigations, and because of the variety of problems offered in each. Realizing, however, that investigations on a few biological groups may easily lead one to draw conclusions that do not apply generally, numerous smaller groups also were included in the experiments. These supplementary investigations have yielded a body of evidence which, in the light of the results surveyed in the previous chapters, gives us added assurance that the principles outlined in the final chapter of this volume are of general biological application.

PHLEUM ALPINUM L.

A great deal of interest centers on this circumpolar species as a result of the investigations of Gregor and Sansome (1930) and Gregor (1931). These involve a cytogenetic and racial analysis of the *Phleum pratense-nodosum-alpinum* complex in Scotland. Among their many findings, Gregor and Sansome discovered that the Scottish *P. alpinum* was tetraploid ($n=14$). Other tetraploid races of this species, later discovered, included two from Swedish Lapland (Müntzing, 1935) and one from Switzerland (Nordenskiöld, 1937). Two diploid forms of *alpinum* ($n=7$) have been discovered, but they were

both in experiment station material of unknown origin; one was found by Gregor and Sansome in a sample of German origin that had arrived via Sweden, the other by Müntzing in Swiss material.

A transplant of *Phleum alpinum* from the edge of a meadow in Slate Creek Valley near Timberline station was included in our cultures. This plant and others in the meadow are tetraploid ($n=14$), like the materials from natural habitats in Scotland, Lapland, and Switzerland, and it shows very regular pairing at meiosis. Accordingly, the tetraploid species, to which the type of Linnaeus' *Phleum alpinum* from Lapland belongs, appears to be the most common and to have the widest distribution, whereas its diploid progenitor probably is native somewhere in Central Europe.

The Sierran *Phleum alpinum* grew poorly at Stanford and scarcely better at Mather, but succeeded well in the garden at Timberline. It grew tallest at Mather and Stanford, as is shown in figure 136 and in the graph, figure 137. The number of stems produced, however, was much the greatest at Timberline, as is shown in table 29. It is early at all three stations and matures seed at Timberline every year. The survival record of this plant is shown in figure 138, and indicates that this form is better fitted to the alpine environment than to that of either of the other stations. The long dry summers at Stanford seem to have an especially detrimental effect, causing the leaves and stems to wither slowly.

SITANION HYSTRIX (NUTT.) J. G. SMITH

Three transplants of this *Sitanion* from Slate Creek Valley were taken into the cultures. The somatic chromosome number in two individuals is $2n=28$, determined in roots. This fits in with the general system of the barley tribe, in which the basic number is 7. This species is widespread in western North America from British Columbia to Mexico. It occurs over a wide range of altitudes and is doubtless differentiated into a number of ecotypes. The transplants of the alpine form demonstrated, in general, better vigor and survival at Stanford and Mather than did those of *Phleum alpinum*, but declined markedly at both of these stations after the second year. At Mather they flowered only one year, and at Stanford the stems became shorter. The clone members at Timberline, on the other hand, showed no evidence of decline. The Mather modifications



FIG. 136. Modifications in clones of alpine *Phleum alpinum* and *Sitanion Hystrix* at three transplant stations.

Plant 1446-1 was raised from seed collected in 1932 near Timberline station. The propagules were planted at Stanford in 1934, and at Mather and Timberline in 1933. Plant 1010-1 was dug at Timberline in 1932, and its propagules planted in 1934. Specimens all taken in 1935.

were the tallest, as is shown in table 29 and in figures 136 and 137. They were also the most prolific in developing culms at this station the single year they flowered, as is clearly shown in the table. In this regard, *Sitanion* was markedly different from *Phleum*, which

produced the highest average number at Timberline. The Timberline race of *Sitanion Hystrix* is one of those alpine which flower late at Stanford. Table 29 shows it to be only three days earlier here than at Mather. The transplants of *Sitanion* were attacked by rust at Stanford, and, like *Phleum alpinum*, suffered obviously during the summers. The survival record of the three clones in culture is shown in figure 138, from which it is evident that the species is able to mature seed successfully at the alpine station.

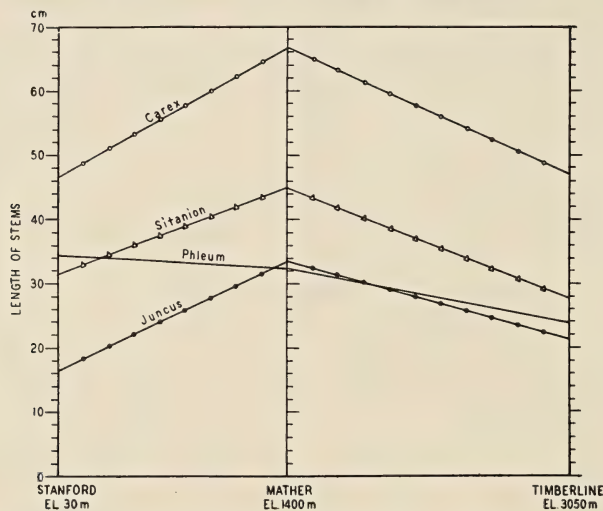


FIG. 137. Modifications in length of stems in clones of alpine *Carex festivella*, *Sitanion Hystrix*, *Phleum alpinum*, and *Juncus Parryi* at three transplant stations.

Graphs based on data averaged from the years 1934 to 1937 for the individuals listed in table 29.

CAREX FESTIVELLA MKZE.

This high-montane member of an assemblage of closely related sedges in the Sierra Nevada and the Rocky Mountains grows in alpine habitats along semi-moist meadow borders. Three transplants from Slate Creek Valley proved to be of exceptional interest in the cultures because of their remarkable vigor under the very different climates at Stanford, Mather, and Timberline. The appearance of clone members of one of these plants after three years at these stations is shown in figure 139. The increase in number of stems and in stature at Mather as compared with either of the other stations is impressive. However, the inflorescences at Mather are attacked by a disease that causes them to wither in the young stages,

the effects of which can be seen in the illustration. Figure 140 depicts the modifications at the three stations as shown by herbarium specimens.

The modifications in length and number of stems and the great differences between the seasons at the three altitudes as reflected in the dates of flowering are shown in table 29. Like alpine forms of *Potentilla glandulosa*, the plants of *Carex festivella* are consistently early at all three stations, and ripen seed in all years at Timberline. The survival graph, figure 138, shows a perfect score for all three

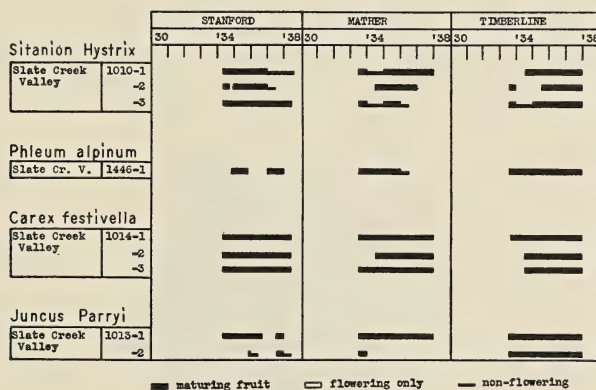


FIG. 138. Record of survival and flowering of clones of alpine *Sitanion*, *Phleum*, *Carex*, and *Juncus* at three transplant stations. See text. The scale indicates years.

individuals at all stations, a record that is indeed unusual, especially for an alpine form of a strictly high-montane species.

In the water-light gardens at Mather the number of stems produced was much greater in the sun than in shade, but their length was not modified appreciably in any of the gardens. The preference of the species for sunny, well-drained places is reflected in its relatively great vigor in the dry sun garden.

The cytology of *Carex festivella* is of interest in connection with that of related *Carices* from other parts of the world. The gametic number is $n=45$, and the chromosomes are very small and roundish, approximately 0.25 micron in diameter. They were observed in first metaphase in pollen mother cells of plant 1014-3. Meiosis is very regular with perfect pairing and well-spaced chromosomes. Material of the circumpolar and closely related *Carex macloviana* d'Urv., from timber line near Abisko in Swedish Lapland, at 850 m. eleva-



AT STANFORD

AT MATHER

AT TIMBERLINE

FIG. 139. Modifications in an alpine clone of *Carex festivella* at three altitudes. This plant, 1014-1, was dug at Timberline in 1932, its propagules planted in 1933, and photographed in 1937.

TABLE 29
MODIFICATIONS IN PHLEUM ALPINUM, SITANION HYSTRIX, CAREX FESTIVELLA, AND JUNCUS PARRYI, ALL NATIVE IN SLATE CREEK VALLEY AT 3050 M. ALTITUDE
(Averages from years between 1934 and 1937)

PLANT NUMBER	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline
<i>Phleum alpinum:</i> 1446-1.....	34.5	32.5	24.0	6.0	5.0	17.5	Apr. 3.0	May 27.5	Aug. 2.0
<i>Sitanion Hystrix:</i> 1010-1..... -2..... -3..... Means.....	42 21 32.0 31.7	45 55 35 45.0	27.5 37.5 18.5 27.8	6.0 3.5 8.3 6.6	75 75 60 70.0	14.0 12.0 2.5 9.5	Jun. 1 Jun. 1 Jun. 18 Jun. 6.6	Jun. 9 Jun. 9 Jun. 11 Jun. 9.6	Aug. 7.7 Aug. 10.5 Aug. 18.0 Aug. 12.1
<i>Carex festivella:</i> 1014-1..... -2..... -3..... Means.....	45.7 49.7 44.2 46.5	71.3 63.8 65.3 66.8	44.5 41.8 54.7 47.0	21.3 22.3 14.8 19.5	81.8 67.5 83.8 77.7	29.0 11.3 30.0 23.4	Apr. 6.7 Apr. 4.7 Apr. 6.7 Apr. 6.0	May 18.3 May 18.3 May 17.5 May 18.0	Jul. 18.3 Jul. 20.0 Jul. 17.7 Jul. 18.7
<i>Juncus Parryi:</i> 1013-1.....	16.3	33.5	20.0	14.3	52.5	30.3	Apr. 15.0	Jun. 8.0	Jul. 27.5

tion, has $2n=ca.$ 82–86 in roots with equally small chromosomes. This does not differ greatly from the Sierran species, in which $2n=90$. Böcher (1938, p. 226) found a similar number in *C. macloviana* from Greenland, i.e., $n=40-41$. Therefore, the similarity between *C. festivella* from the arctic-alpine zone in the Sierra Nevada at 38° N. and *C. macloviana* from Lapland at 68° N. and from Greenland extends to the number and size of the chromosomes as well as to grosser morphological characters. This similarity is of special significance because these two have a far higher number of chromosomes than other species of the subgenus *Vignea*, which, as shown by Heilborn (1924, 1928), otherwise consists of species having but 26 to 34 pairs.

Twenty-one plants of a seedling culture of *Carex macloviana* from Lapland have been grown in the garden at Stanford. They show a striking reduction in size of all parts, including length of stem, in contrast to the Sierran *C. festivella*, which was not so reduced when transplanted from Timberline to Stanford. The scapes of *C. macloviana* at Stanford are decumbent-ascending and only 15 to 20 cm. long as contrasted with the erect scapes 25 to 42 cm. long on the parental plants in Lapland.

JUNCUS PARRYI ENGELM.

This rush abounds in the vicinity of Timberline station on glacial moraines and well-drained, sunny slopes. Two transplant individuals reacted in general like *Carex festivella*, but did not show as much relative vigor at the lower altitudes. The modifications at the three transplant stations are illustrated by herbarium specimens in figure 140, while the mean lengths of flowering stems are shown in figure 137. The garden cultures indicate clearly that the species thrives far better at Timberline than at Mather or Stanford in spite of its taller stature and its larger number of stems at the mid-altitude station. This is reflected somewhat in the survival graph, figure 138. Although on the average a somewhat greater number of flowering stems has been produced at Mather, the clone members at Timberline have bloomed more consistently, and, like true alpine species, have produced ripe fruit there even in the shortest seasons. For an alpine species this *Juncus* was late at Mather, as is shown in table 29, but it was early at both Stanford and Timberline. In the water-light

Juncus
1013-1



dm

Carex
1014-1



at Stanford
El. 30 m

at Mather
El. 1400 m

at Timberline
El. 3050 m

FIG. 140. Modifications at three altitudes in clones of *Juncus Parryi* and *Carex festivella*.

Plants 1013-1 and 1014-1 were both dug at Timberline in 1932, and their propagules planted in 1933. The specimens were taken of 1013-1 in 1935, of 1014-1 in 1937.

gardens at Mather, only half as many stems were produced in the shade as in the sun, on the average, but except for this expression of difference in vigor, little modification was observed in clone members in this series of gardens.

SISYRINCHIUM BELLUM WATS.

Prominent among the spring-flowering plants of California is this species of the iris family. It grows in meadows and open slopes throughout the state, having an altitudinal range from sea level to timber line. Its many forms vary in such characters as width of stems and leaves, pubescence, color shade, size and number of flowers, earliness, stature, habit, and vigor.

DIVERSITY WITHIN THE SPECIES. In our transect we have found a series of ecotypes as diverse as the *Potentillas*, *Artemisias*, and *Achilleas*. A maritime ecotype occurs along the immediate coast—a broad-leaved form of relatively low habit with scapes barely surpassing the leaves, and with prominent bracts and large-petaled purple flowers borne in relatively large number on each stem. Inland, in the valleys and on the slopes of the Coast Ranges, one finds a somewhat taller form with scapes markedly surpassing the narrower leaves, and blue flowers. In the upper foothills and middle altitudes of the Sierra Nevada, a form of more slender habit than any from the coastal region is found, while at high elevations, even approaching timber line on the crest of the Sierra Nevada, one finds dwarfs with narrow leaves and short, slender stems bearing but one or very few flowers. The eastern slope of the Sierra Nevada is inhabited by forms that become increasingly taller the lower the altitude until, in the Great Basin, one finds the species as a narrow-leaved, rather slender form of moderate stature and with light blue flowers growing in the moister meadows, even in those that are subsaline. All these forms have 16 pairs of chromosomes.

RESULTS FROM THE VARIED-ENVIRONMENT STUDIES. Transplants of this species have been grown in limited numbers, sufficient, however, to demonstrate that forms from different altitudes differ in their capacity to survive at Stanford, Mather, and Timberline.

Plants of the maritime ecotype originally from Montara, California, thrive luxuriantly at Stanford, producing many stems and a massive

growth, but at Mather they are nearly winter-killed, produce but little growth and few stems, and usually fail to survive more than a year or two. In seven attempts they have never survived a winter at Timberline. Plants of the Mather ecotype, on the other hand, thrive both at Stanford and at Mather and were even able to produce immature flowering stems at Timberline in one year, although they do not survive well there. Alpine races from Tuolumne Meadows or Slate Creek Valley live with difficulty at Stanford or Mather. A form from near Mono Lake, in the Great Basin, has been too recently acquired to warrant a full report, but from present evidence it appears to thrive quite successfully at all three stations.

The maritime, mid-Sierran, alpine, and Great Basin forms of *Sisyrinchium* are represented in figure 141 through the vertical comparisons, while the clone members of these races at the three transplant stations are shown in the horizontal series of pictures. At Stanford one sees most clearly the morphological contrasts between the different ecotypes as they appear in the same garden. The alpine is the dwarfest, and the mid-Sierran the tallest, while the maritime form has a characteristic rather low, spreading aspect. The Great Basin form resembles the alpine but is taller in stature. At Timberline only the alpine and Great Basin forms prosper; the mid-Sierran is just able to flower there and the maritime plant does not survive. The data at Mather are incomplete for the alpine and Great Basin forms, hence they are not shown. The differences in reaction between the maritime and the mid-Sierran forms at this mid-altitude station show the weakened condition of the maritime plant as expressed in its greatly reduced stature, its much more limited production of stems, and the narrowing and shortening of the leaves. In contrast, the mid-Sierran race, at home in its native environs, grows with normal vigor.

Some of the differences in reaction between the maritime and mid-Sierran races are clearly brought out in table 30. Especially noteworthy is the great reduction in number of stems produced by the maritime ecotype at Mather as compared with Stanford. Also, at Stanford the maritime ecotype is the earliest to flower, whereas at Mather it is the latest. This is comparable to maritime plants of other groups, previously mentioned.

At Stanford, the maritime form begins the new season's growth in the late fall, with the coming of the winter rains, and continues

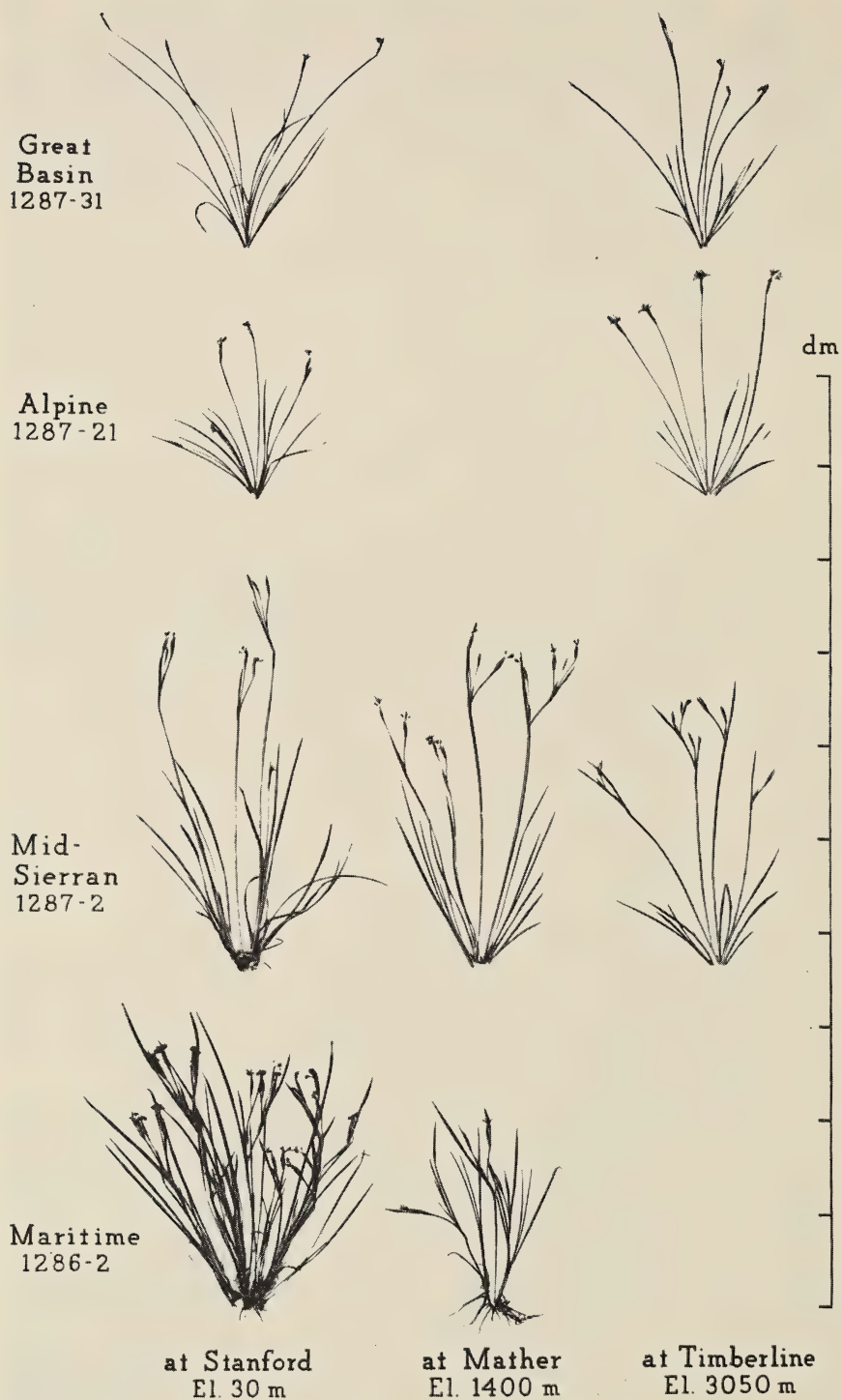


FIG. 141
(Legend on opposite page)

to develop steadily until April, the time of flowering. Following the ripening of the seed in June, these plants gradually wither and pass into a dormant period which lasts through the dry late summer and early fall. The Mather ecotype, on the other hand, remains dormant at Stanford until the middle of January, and with this later start does not come into flower as early as the maritime; otherwise, its seasonal cycle is similar. At Mather both ecotypes begin spring growth simultaneously, the mid-Sierran form with vigor, the maritime very slowly because of an obvious weakening that it has suffered during the winter. Moreover, the maritime form is less resistant to spring frosts and may succumb before flowering, but if it survives the critical spring period, it gradually increases in strength as the summer progresses.

CYTOLOGY. As was mentioned earlier, the chromosome number of the various ecotypes of *Sisyrinchium* is the same, i.e., $n=16$. The following plants have been studied cytologically. Most of the counts were made in roots, but the asterisk indicates that the number was also determined in meiosis.

Sisyrinchium bellum S. Wats., $n=16$:

Maritime form, 1286-1* and -2, Point Montara, San Mateo Co., elevation 15 m.

Mid-Sierran form, 1287-1 and -2, Mather, Tuolumne Co., 1400 m.

Alpine form, 1287-21, Slate Creek Valley, Mono Co., 3050 m.

Great Basin form, 1287-31, Farrington's, south of Mono Lake, 2070 m.

It is clear from these incomplete studies on *Sisyrinchium bellum* that this widely distributed species is differentiated into ecotypes fitted to different kinds of environment, as has been already so clearly seen in *Potentilla*, *Zauschneria*, *Achillea*, and *Artemisia*.

FIG. 141. Modifications at three altitudes in clones representing altitudinal races of *Sisyrinchium bellum* from California. All have the same chromosome number, $n=16$.

1286-2, dug March 30, 1922, at Point Montara, San Mateo County, near sea level; the propagules were planted at Stanford in 1929 (grown at Berkeley 1922-1929), at Mather in 1936 (replanted). It did not survive at Timberline. Both specimens taken in 1938.

1287-2, dug June 24, 1933, near Mather; the propagules were planted at Stanford and Mather in 1934, and at Timberline in 1937 (for the second time). Specimens taken in 1937 at Stanford, and in 1938 at Mather and Timberline.

1287-21, dug September 7, 1934, at Timberline station; the propagules were planted at Stanford in 1937 (reset), and at Timberline in 1936. Specimens taken in 1938 at Stanford and in 1937 at Timberline.

1287-31, dug July 3, 1936, near Mono Lake, Mono County, at 2070 m. The propagules were planted in 1937 and specimens taken in 1938.

TABLE 30
MODIFICATIONS IN SISYRINCHUM BELLUM
(Averages from four years, 1934 to 1937)

NUMBER AND ORIGIN OF PLANTS	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS			
	Stan- ford	Mather	Timber- line	Stan- ford	Mather	Timber- line	Stanford	Mather	Timberline	
MARITIME:										
	1286-1, Montara.....	20.4	25.0	60.4	10.0	Apr. 23.0	Jun. 15.0
	-2, Same.....	27.2	15.0	124.0	7.5	Apr. 3.0	Jun. 6.0
	-3, Same.....	20.8	12.0	117.0	40.0	Mar. 31.3	Jun. 1.0
	Means.....	22.8	17.3	100.5	19.2	Apr. 8.8	Jun. 7.3
MID-SIERRAN:										
	1287-1, Mather.....	40.5	29.0	27.0	19.5	17.0	15.0	Apr. 16.3	May 31.8	Sep. 10.0
	-2, Same.....	36.0	28.3	29.0	35.6	17.0	25.0	Apr. 18.5	May 31.0	Sep. 10.0
	Means.....	38.3	28.7	28.0	27.6	17.0	20.0	Apr. 17.4	May 31.4	Sep. 10.0

This species of *Sisyrinchium* apparently compares with *Potentilla glandulosa* in composition, since its wide diversity of forms has evolved without a change in chromosome number. The group merits further study.

THALICTRUM FENDLERI ENGELM.

Along with other Ranunculaceae, the genus *Thalictrum* has attracted wide interest because of its cytological complexity, chiefly its polyploidy (see Langlet, 1927; Kuhn, 1930). In the Sierra Nevada along our transect occurs a group of apparently complex composition referable to *Thalictrum Fendleri*. This is a montane species found from California to the Rocky Mountains. Two forms, one mid-Sierran and the other alpine, are shown in figure 142. Both races are dioecious, male and female plants occurring in about equal numbers in both. The alpine is tetraploid, $2n=28$, determined in roots of two plants, a male and a female. This is the same number as that found by Langlet and Kuhn in botanical garden forms of *Thalictrum Fendleri*. The Mather race, as is shown in the illustration, is a very tall, relatively coarse-textured form with a higher number of chromosomes that seems to vary among different individuals. One plant (1289-2 of fig. 142) was octoploid, $2n=56$, while another from the same population was decaploid, $2n=ca. 70$. One may be led to suppose that the Mather form is apomictic, but this point needs further investigation.

Both the alpine and the Mather races of *Thalictrum* grow poorly at Stanford, for these moisture-loving meadow plants suffer there so much from drought that, even with irrigation, they scarcely flower, or, if they do, their development is decidedly stunted. Brought to Timberline, the Mather race survives for a year or two, but becomes progressively weaker and dies, showing a reaction not unlike that of the pentaploid *Achillea* represented in figure 123. The alpine race, of course, thrives at Timberline station, where it is in its native environs. It also grows well at Mather, and with but little modification.

In the water-light gardens at Mather the effects of sun and shade are quite characteristic. Sun causes thick, sturdy, erect stems to develop in the Mather race, while shade makes them so thin and weak that they fall to the ground under their own weight. The moist gardens favor their development better than the dry. Both



FIG. 142. Mid-Sierran and alpine races of *Thalictum Fendleri* grown in a uniform garden at Mather.

Plant 1289-2 was dug in 1926 near Mather at 1400 m.; 1290-4 was dug in 1934 near Timberline station at 3050 m. Specimens of 1937.

the alpine and the Mather form produce fewer flowers, or none at all, in shade.

So in *Thalictrum* we have glimpses of a pattern of differentiation not unlike that of other groups, but associated with chromosome differences and probably complicated by the existence of apomixis in some of the forms. Further experimental investigation of the west American *Thalictrums* would doubtless clarify the relationships of a group which has long perplexed systematists.

SPECIES OF CRASSULACEAE

A plant of *Echeveria Cotyledon* (Jacq.) Nels. & Macbr., a species confined to the ocean-facing bluffs along the coast of central and northern California, was collected near Monterey and transplanted to the three stations. After the second year it was abandoned as a transplant because it was very evident that the species was unable to survive the winters either at Mather or at Timberline. At Stanford it grows vigorously.

Sedum spathulifolium Hook., a species common in rocky places in California from near sea level to mid-altitudes, was taken as a transplant at Albion Ridge, Mendocino County, on a bluff overlooking the ocean. This coastal race was very prolific and lived successfully at Stanford and Mather, but failed to survive more than one winter at Timberline. No modifications worthy of note were observed in these succulent transplants. Two plants of this species, originally from Mather, grew so slowly at all three stations that they were difficult to establish in culture. Only at Stanford did they survive for two years.

In contrast to these two species, transplants of *Sedum obtusatum* Gray from Timberline have survived very well at all three stations during the six years they have been in culture. At Stanford they grow slowly and steadily throughout the year in dry seasons as well as moist. No modifications worth mentioning have been observed, the species being very stable in its characters. These three species of Crassulaceae have therefore very different capacities for survival at different altitudes.

SPECIES OF GERANIUM

Geranium incisum Nutt. occurs in the Sierra Nevada at elevations between 800 and 2100 m., while *G. Richardsonii* Fisch. & Trautv.

grows at higher altitudes, from 1700 to 2700 m. The former species has rose-pink flowers, while those of the latter are white. *Geranium incisum* generally is more pubescent, of less slender habit, and has a tendency to produce smaller basal leaves with shorter petioles than does *G. Richardsonii*. Otherwise, the two resemble each other rather closely.

One object of the transplant studies in these species was to determine the relative stability of the characters differentiating them. In an early experiment started in 1922, five individuals of *Richardsonii* from Porcupine Flat, Yosemite National Park, elevation 2450 m., were moved down to Mather at 1400 m. and set into the holes left by the removal of five plants of *incisum*. These plants of *incisum* were then transplanted reciprocally into the exact locations previously occupied by the plants of *Richardsonii*.

Geranium Richardsonii retained all its characteristics at Mather as long as the transplant survived, that is, for five to ten years. Likewise, the individuals of *G. incisum* moved to Porcupine Flat, while modified slightly, retained the characters of that species and the peculiarities of the various individuals up to 1929, seven years later; then they were again moved higher up the mountains to Timberline. Here they became markedly dwarfer in stature, producing shorter stems, shorter petioles, and smaller and thicker leaves. This reduction was noticed the first year after transplanting. Records from subsequent years indicate no further modification, even until as late as 1937, the date of the last survivor. The plants of *incisum* brought to Timberline in no way lost their individuality, for the dwarfing effect involved no change in the pattern of the parts concerned. Certainly, *incisum* had taken on none of the characteristics of *Richardsonii*, either at Porcupine Flat, where the latter species occurs in abundance, or at Timberline, above the natural range of both species.

Clone members of *incisum* from Mather were slightly modified as to form when moved to Berkeley, having somewhat heavier and darker green leaves, and slightly shorter flowering stems, but they were more strikingly changed in their seasonal reactions. They flowered over extended periods and were noted to be in flower almost continuously through the year. This particular reaction has not been duplicated in any other species in the experiments. The several clone members of *incisum* grew well in the relatively cool, humid

climate at Berkeley, but did poorly when brought to the more arid climate at Stanford.

A plant of *Geranium caespitosum* James, originally from Minnehaha, Pikes Peak, Colorado, brought to Mather in 1922, retained its original characteristics for ten years after transplanting. The length of flowering stems, mode of branching, relative lengths of internodes, size and arrangement of cauline leaves, thickness and texture of stems and leaves, and leaf veining remained unchanged, as evidenced by a careful study of the herbarium specimens taken before and after transplanting. A slight increase in glandular pubescence, and some tendency for basal leaves to become further subdivided, are the only modifications observed. The small morphological differences which distinguish the Colorado plant from the closely related *G. incisum* native at Mather are retained.

VIOLA ADUNCA J. E. SMITH AND ITS RELATIVES

One of the most widely distributed groups of violets in the United States is the *Viola adunca* complex. These purple-flowered members of the *Nomimium-Rostellatae* subsection are related to the Eurasiatic *Viola rupestris* Schmidt and *Viola silvestris* Reichb. It is not known whether the *adunca* complex constitutes one or several species. So far as is known, all the members are diploid, $n=10$, like their Eurasiatic relatives *V. rupestris* and *silvestris* (Clausen, 1927, 1929). This complex ranges from California to Alaska and eastward through the Rockies to the Atlantic in Quebec and New England, where its members are sometimes listed under the name *V. canina* L.

The type form of the *adunca* complex occupies a long montane strip near the Pacific northward and southward from Puget Sound. Another form, ssp. *oxyceras* (Wats.) Piper, appears at mid-altitudes in the Sierras, extending up to about 2800 m., no real alpine form having been developed here. Various forms are found through the lower parts of the mountains from eastern Oregon and Washington eastward, including the larger-leaved *V. montanensis* Rydb. They grade into smaller forms at higher altitudes, until they merge into the alpine and very dwarfish *V. bellidifolia* Greene, at 2500 to 3400 m. in the Wasatch and the Rocky Mountains.

TRANSPLANT REACTIONS. Two forms of this complex have been included in the transplant experiments. They are the typical coastal

Viola adunca from near Montara, San Mateo County, and var. *oxyceras* from Mather in the Sierras at 1400 m. altitude. The Montara plant became dormant for a short period in the late summer and fall near its native habitat at Stanford, and resumed the next season's growth in November during the rainy period. Flowers appeared freely from February until May. A clone member brought to Mather began spring growth unusually early for a coastal plant, starting to bloom in the latter part of May. Another at Timberline survived two winters in the slope garden, which is unusual for a plant from the coast, and, though very weak, even flowered one summer.

A plant of ssp. *oxyceras* from Mather thrived at Stanford for two years and then died. Characteristically enough, it remained green in the late summer and fall while the coastal *adunca* was in a resting stage, but became dormant for a very short period in midwinter while *adunca* was resuming new growth in response to the rains. Consequently, ssp. *oxyceras* flowered about three weeks later than the coastal plant. Both forms were short-lived in the cultures, so little can be said regarding their relative survival capacities at the transplant stations.

The Sierran and the coastal forms are distinct both in their morphology and in their reactions. Because they are not different in chromosome number and their ability to hybridize is not known, we cannot decide whether they are two ecotypes of one ecospecies or two closely related ecospecies. The morphological differences between them are not spectacular, however.

CYTOLOGY. Mr. Milo S. Baker, of the Santa Rosa Junior College, and the authors have fixed material of the *Viola adunca* complex in the wild and in the transplant gardens. Mr. Baker has grown several of the forms in his garden at Kenwood (Baker, 1936) and is to publish the taxonomic treatment of this group.

The chromosome counts were made mainly on bud material; an asterisk in the list below indicates that meiosis was investigated. In other cases the chromosomes were counted in somatic divisions in buds.

Viola adunca J. E. Smith, diploid, $n=10$:

The coastal form, ssp. *typica* M. S. Baker:

1817-2*, Montara Mt., San Mateo Co., 150 m. (a transplant).

San Bruno Hills*, San Mateo Co., ca. 125 m. (Clausen, 1929).

Hills south of Tomales Bay*, Marin Co., *ca.* 200 m. (Clausen, 1929).

1828-1, Albion Ridge, Mendocino Co., *ca.* 75 m. (a transplant).

Baker*, transplant from Vancouver Island, British Columbia.

ssp. *oxyceras* Piper:

1829-1*, Mather, Tuolumne Co., 1400 m. (a transplant).

Baker, transplant from Big Bend Ranger Station, Nevada Co., 1850 m.

Baker, from Donner Lake, Nevada Co., 1830 m.

Keck 3659, near Dixie Pass, Grant Co., Oregon, 1280 m.

Baker 7398, near Lewiston, Idaho, *ca.* 225 m. (*retroscabra* Greene).

ssp. *Ashtonae* M. S. Baker:

Baker 5430*, Cub Lake trail, Rocky Mountain National Park, Colorado, 2550 m.

ssp. *radicosa* M. S. Baker:

Baker 4772, Kewuneeche Valley, Rocky Mountain National Park, Colorado; the type number of the subspecies.

REACTIONS OF EUROPEAN RELATIVES OF *VIOLA ADUNCA* AT STANFORD.

In comparison with the California *Viola adunca*, it is of interest to consider the reaction of two north European tetraploid relatives. They are *Viola Riviniana* Reichb. and *V. canina* L.; both have $n=ca.$ 20 chromosomes (Clausen, 1927, 1931). Several seedling cultures of these were raised at Stanford.

Viola Riviniana is native in the European deciduous forests, whereas the superficially similar but smaller *V. canina* grows on open grassy hills, meadows, and moors. The winter behavior of the two at Stanford is quite different. *Viola Riviniana*, in harmony with its occurrence in the protected forests, stays evergreen throughout the winter. *Viola canina*, on the other hand, goes completely dormant in the late fall and does not appear again before March or April, depending on the earliness of the season. It is of interest that both species, started as seedlings in California, have preserved this difference in rhythm for six years. No adaptation to the Stanford climate can be claimed in this case, and the fact that *Riviniana* is grown in an open, unprotected garden does not alter its reaction.

Two cultures of *V. Riviniana* were grown; one, consisting of ten individuals, was from a Danish forest in South Jutland; the other, of twenty-five plants, was raised from seed collected by Dr. J. W. Gregor in an open moorland pasture at Killin, Perthshire, Scotland. Likewise two cultures of *V. canina* were grown; one, of twelve individuals, was raised from seeds of the Bidstrup population, north of Copenhagen, and the other, of twelve plants, originated from the Ljungby

population from a moor in Småland, southern Sweden (Clausen, 1931). The Swedish population of *canina*, from a locality about 160 kilometers farther north than the Danish, and from a more continental climate, emerges from dormancy one to three weeks later than the Danish.

The races of *V. Riviniana* and *canina* are very vigorous and floriferous at Stanford, and attain the same size as in northern Europe. They survive for a considerably longer period than their California relative, *Viola adunca*.

EPILOBIUM ANGUSTIFOLIUM L.

The purple fireweed, *Epilobium angustifolium*, occurs in temperate regions in the three continents of the Northern Hemisphere. Considering this very wide distribution, it is a species of remarkable morphological uniformity. However, in the Sierra Nevada there is a striking inverse correlation between the stature of its forms and the altitudes of their habitats. Along our transect it grows from 600 m. elevation to above timber line at 3350 m. Races from lower altitudes develop robust stems that become 10 to 15 dm. tall, but the alpine types produce much more delicate ones only 2 to 5 dm. tall. Nanism becomes most apparent in the upper 300 m. of the range, although plants from 2400 m. upward show tendencies in this direction.

Transplant experiments at Mather and the coastal stations demonstrate definitely the hereditary nature of the differences between mid-Sierran and alpine races. When dwarfs from Tioga Pass at 3020 m. are grown beside tall forms from Mather at either Stanford or Mather, their original characteristics are retained. The striking differences in height, size of leaves, inflorescences, and flowers, thickness of stems, and number of internodes continue to be as pronounced five years after cultivation as before the experiments were begun.

Alpine types mature much more rapidly during a growing season than do individuals from Mather. At the coastal stations, Mather forms start spring growth earlier, sending out new shoots from subterranean rootstocks around the middle of March, while transplants from Tioga Pass do not show signs of activity until the first of May. By the first part of July, however, when the mid-altitude forms are in flower, the alpiners already have mature fruit. At Mather similar

differences in rates of seasonal development are evident, so that in mid-August, when plants from Tioga Pass are shedding seed, natives from Mather are just beginning to flower.

It should not be inferred from the preceding paragraphs that modifications in *E. angustifolium* may not be striking. Forms from north Scandinavia raised as seedling cultures at Stanford grow to only a fraction of the size of the plants in their native habitats. Below are listed the results experienced with four cultures.

Origin of plants	Height in native habitat (cm.)	Height at Stanford 38°N. (cm.)	Number of plants set at Stanford	Plants sur- viving first winter
Skärålid, Skåne, Sweden, 56° N....	150-230	15-63	32	14
Piikkiö, near Åbo, Finland, 60° N..	150-175	5-40	28	7
Uppsala, Sweden, 60° N.	115	3-20	26	6
Abisko, Lapland, Sweden, 68° 20' N.	60-100	14	None

From these results it is evident that the races show marked declines at Stanford that become progressively greater in those of more northern origin. It is remarkable that it was apparently the mild Stanford winter that killed them. They grew vigorously in a cool, shaded lathhouse during the first summer; they were then planted in the garden from large pots and became well established before they went into winter dormancy, from which not one of the Lapland plants emerged. Heights at Stanford were measured in the garden the second season.

In this connection it is of interest that a seedling culture of *E. latifolium* L., originally from Disko, northeast Greenland, at 69° N., was unable to survive even the first summer at Stanford, although the plants were kept in the lathhouse. This was the race used by D. Müller (1928) for his assimilation experiments at Disko. Müller brought this race to the Copenhagen Botanical Gardens at 55° 40' N., where it flourished in the open, although this species does not occur in Europe except on the arctic islands north of the continent. The seeds for the Stanford culture came from the Copenhagen plants. The germination was quite good, and about thirty seedlings were obtained, which developed into weak plants with very slender stems. Nine of them survived from spring until late summer, but they became dormant early, and none survived the winter. *Epilobium latifolium* is reported from the Sierra Nevada in California. This

race probably is physiologically very different from the Greenland race, 31° farther north.

Clements (1926) reported a transformation of *E. angustifolium*, a species with subterranean stolons, into *E. latifolium*, a species with a subterranean corm. This transformation would be a very startling one, unless it is to be interpreted as meaning only that the leaves of *angustifolia* had widened in shade.

DODECATHEON JEFFREYI MOORE AND *D. ALPINUM* GREENE

The shooting stars are abundant in boggy meadows in the Sierra Nevada. *Dodecatheon Jeffreyi* Moore grows at elevations from 1250 to 3000 m.; at the lower altitudes in typical form it grows from 50 to 85 cm. tall, while at the upper limits of its distribution it reaches only 10 to 20 cm. and is referable to forma *pygmaeum* Hall. Transitional types grow at intermediate elevations.

Dodecatheon alpinum Greene is smaller in all its parts and is glabrous throughout, whereas *D. Jeffreyi* has glandular stems and pedicels. Its altitudinal range in our transect lies between 2400 and 3350 m., and, as in *D. Jeffreyi*, the tallest forms occur at the lowest altitudes, where they are 15 to 30 cm. tall, while the shortest (only 5 to 15 cm. tall) grow at the highest elevations and are referable to forma *nanum* Hall. This species frequently occurs together with *D. Jeffreyi* and yet it appears to remain distinct, notwithstanding the fact that the two resemble each other morphologically.

RESULTS FROM TRANSPLANTING. Dr. H. L. Mason, now of the University of California, became especially interested in *Dodecatheon* transplants while working with Dr. Hall from 1923 to 1925. Through their joint efforts, approximately one hundred individuals of this genus were taken into culture from different altitudes between Mather and Tioga Pass.

Figure 143 illustrates an experiment that summarizes the most important results from this work. An individual of *Jeffreyi*, taken from its original habitat at Mather at 1400 m., first to Tuolumne Meadows at 2650 m. for a period of seven years under subalpine conditions, and later to Timberline at 3050 m. for an additional three years under alpine influences, has retained its original characteristics except for some reduction in length of stems and in number of flowers

From this and similar experiments it is obvious that plants of *Jeffreyi* from a low altitude, subjected to the environmental impacts natural to *alpinum* at high elevations, not only fail to assume the characteristics of that species, but even show relatively little modification in length of stems or size of leaves. The modifications which do result, such as a small but definite reduction in length of scapes and a slight decrease in size of leaves, are only of a temporary nature and reflect the plant's immediate vegetative adjustments to changed climates. General size, shape, venation, and relative numbers of rosette leaves, color, shape, and size of flowers, density of pubescence, and habit serve to identify individual transplants at any of the altitudes, for these characters are not modified or are changed relatively little.

A few individuals of *Jeffreyi*, originally from Mather, were planted at Snow Flat in especially wet, boggy places where they stood in water several centimeters deep during spring and early summer. The submerged portions of the basal leaves became narrower and less green than corresponding parts of leaves of plants not standing in water. This change in leaf shape due to submergence varied according to the depth of water. After the same plants were moved to Timberline to well-drained gardens, they produced basal leaves of normal shape and color. These modifications are of interest because leaf shape has been used as a taxonomic character in this group of Dodecatheons.

Transplants of *Dodecatheon alpinum* appear very stable in their characters. Reciprocal exchanges between White Wolf (elevation 2440 m.) and Tuolumne Meadows (elevation 2650 m.), and between these places and Tioga Pass (elevation 3050 m.), have failed to induce noticeable differences in stature, size or shape of leaves, or number of flowers per stem. Likewise, only very minor modifications appear in plants brought from high elevations to Mather. The limited number of survivors there suggests that the physiological limits beyond which adaptation is impossible are quite as strict as the limits of structural modifiability.

MONARDELLA VILLOSA BENTH. AND M. ODORATISSIMA BENTH.

Many transplants have been made of the perennial Monardellas of California. Interest has been largely confined to members of the

polymorphic species *Monardella villosa* and *M. odoratissima*, both of which undergo their greatest differentiation in California. In his monograph of the genus, Epling (1925) recognizes several subspecies under each of these. Some of this variation is found in both species in the vicinity of the transplant station transect. In this area *villosa* is principally confined to the Coast Ranges and *odoratissima* to the Sierra Nevada. Typical reactions of each species at the three stations are discussed below.

Transplants of *Monardella villosa* originally from the Coast when grown at Berkeley or Stanford become 30 to 60 cm. high, and their perennial stems become woody. Numerous inflorescences arise as side branches, so that vigorous, well-rounded specimens are produced. There are two flowering periods each year at the coastal stations, one in spring and another in fall, while growth of foliage occurs throughout the year.

In contrast to this continuous activity, transplants from the coast grown at Mather are forced into winter dormancy from October until the first of May, and snows and freezing weather kill most of the aerial branches, which normally are perennial. Spring growth begins with the unfolding of over-wintering buds situated at the bases of the winter-killed main branches, or near the central crown of the plant below the ground. The new growth is often injured repeatedly by late frosts. The surviving stems, however, produce inflorescences, but coastal plants at Mather are weaker and much less woody than the Berkeley or Stanford clone members that stay evergreen. Clones which average 50 cm. in height at Stanford become but 20 or 25 cm. high at Mather, and have many less flowering stems. There is only one short flowering period at Mather, after which October freezing weather induces dormancy. Thus, the coastal *Monardellas* react much like the woody *Zauschnerias* from the coast, as described in chapter VI.

Morphological characters of clone members of the coastal *M. villosa* grown at the coastal stations and at Mather are alike in corresponding parts of similar age except for minor textural differences. Leaves developed at the coastal stations usually are darker green, especially at Berkeley, and are somewhat thicker and more heavily veined; also they tend to be more pubescent. Flower and inflorescence characters appear to be identical at the two stations, except that stems are thicker and better developed at Berkeley and Stanford.

All attempts to grow coastal forms of *villosa* at high altitudes, such as at Tuolumne Meadows and at Timberline, have failed, for propagules set out during a given summer are winter-killed the first year.

Both at Stanford and at Mather the effect of growing clone members of *M. villosa* from the coast in sun and shade is similar. Plants in shade have longer internodes and develop thinner and larger leaves whose density of pubescence is often considerably reduced. Fewer flowers and, in general, less vigorous plants are produced in moderate shade, while heavy shade inhibits flowering altogether.

Forms of the Sierran species, *M. odoratissima*, from Tuolumne Meadows, transplanted to open gardens at Mather, seem to suffer from heat during the warm summers, but if grown in gardens partly shaded by pines, they thrive quite well. Individuals thus grown for as long as seven years have not changed their original characters in any appreciable degree. Clone members of *odoratissima* originally from high altitudes have invariably died at Berkeley or Stanford, if not after the first year, then after the second or third.

ERIGERON SALSUGINOSUS GRAY

This widely distributed daisy is abundant in Sierran meadows at elevations ranging between 1650 and 3350 m. Although approximately forty transplant individuals were taken along the transect between Mather and Timberline, the data are fragmentary because these plants are too delicate to propagate successfully by vegetative means. Very few clone members have been grown at Berkeley or Stanford.

In some of the early experiments, transplants originally from Tuolumne Meadows (elevation 2650 m.), of an average height of 20 to 25 cm., were moved to Porcupine Flat (elevation 2500 m.), where they increased to an average of 30 cm. After seven years the survivors were retransplanted up the mountains to Timberline station (elevation 3050 m.), where, two years later, their stature was found reduced to 10 to 13 cm. Basal and cauline leaves followed the trend of the stature.

Plants from Tuolumne Meadows brought to Mather were greatly influenced by differences in sun and shade. Propagules in moist shaded gardens became 30 to 40 cm. tall, while those in moist sun reached a height of only 10 to 16 cm. the same year. The shaded

plants had larger leaves, and there was a distinct tendency for inflorescences to branch and to produce more flowers per stem. In the wild, *Erigeron salsuginosus* often grows in partly shaded meadows, so it is not surprising that transplants brought to Mather at an elevation below the natural range of the species thrived best in shaded gardens.

Individuals from the same meadow often vary in the amount of pubescence on stems and leaves. One of the objects of the transplant experiments with this species was to determine to what extent these differences were hereditary, and to what extent modificatory. Accordingly, series of plants varying from nearly glabrous to grayish-pubescent were dug at Porcupine Flat and at Tuolumne Meadows and transplanted to Mather in uniform gardens, both sun and shade. There they retained their original differences in density of pubescence as long as they were in culture, i.e., up to five years.

SOLIDAGO ELONGATA NUTT. AND *S. MULTIRADIATA* AIT.

These two widespread species complexes occur along the transplant transect at different ranges of altitude. *Solidago elongata* grows from British Columbia and Montana southward to Utah and California. In the Sierra Nevada it occurs from 900 to 2300 m. The *S. multiradiata* complex belongs to higher altitudes and latitudes; in the Sierras it grows between 2600 and 3600 m., and it extends northward to the Aleutian Islands and Hudson Bay. The California forms of the latter are usually referred to as *S. corymbosa* Nutt., a name invalidated by the earlier *S. corymbosa* Ell. Some evidence suggests that both of these species complexes in California are differentiated into altitudinal ecotypes, but further field and experimental studies are needed to determine what variability occurs.

Several individuals of *elongata* from Mather (elevation 1400 m.) have been studied as transplants. The most important results from these are pictorially summarized in figure 144, showing living representatives of a clone at the three transplant stations, and figure 145, showing herbarium specimens. The clone members at Stanford, as compared with those at Mather, are strikingly dwarfed in stature. Their much-shortened flowering stems have smaller and more densely spicate inflorescences, shorter internodes, and wider, thicker, and more coarsely veined leaves. The Stanford plants are not nearly so vigorous as the propagules at Mather; they produce fewer stems, and



FIG. 144. Modifications in a clone of mid-altitude *Solidago elongata* at Stanford (below), Mather (center), and Timberline (above).

This plant, 1310-3, was dug November 3, 1926, near Mather. The propagule at Stanford was brought from Berkeley in 1929, where it had been growing since 1927; the divisions at Mather and Timberline were taken from Stanford and planted in 1933. Photographed in 1937 and reproduced to the same scale.



FIG. 145. Modifications in a clone of mid-altitude *Solidago elongata* at three altitudes. The histories of the propagules of plant 1310-2 are essentially the same as for 1310-3 in figure 144. The propagule of 1310-2 at Mather has a branched inflorescence caused by insect injury to the terminal bud, while 1310-1 is normal.

often have difficulty in surviving, although they may become well established.

These modifications take place immediately after the propagules are brought to Stanford. Thus, another root division from a plant at Mather like that shown in figure 144 produced the characteristic dwarf stems at Stanford the same summer that it was transplanted.

The inflorescence of *S. elongata* normally is a congested ovoid panicle consisting of a central axis from which arise side branches bearing dense spiciform racemes of heads (fig. 145, 1310-1). At Mather the growing points often are destroyed by insect larvae when the shoots are half-grown. This stimulates the axillary buds to develop into new side branches, each of which develops a spiciform panicle of heads. The result is the production of a freely branched flowering stem (fig. 145, 1310-2 at Mather). Both this and the normal type may be found on the same clone member at Mather, as is shown in figure 144, but larvae causing terminal bud injury prefer propagules in shaded or semi-shaded gardens to those in dry, sunny plots (Hall, 1926). The recent researches on phytohormones (summarized by Went and Thimann, 1937) now explain the relation between injury to terminal buds and the development of side shoots.

At Timberline *S. elongata* from Mather produces only immature shoots, as is shown in the figures. There the plants may survive for several years through the activity of the persistent underground rootstocks, but eventually the propagules become weak and die. The clone member at Timberline shown in figure 144 is obviously in its last season of survival.

When *S. multiradiata* from Tioga Pass (elevation 3030 m.) is transplanted to the three stations, it reacts in a very different manner from *S. elongata*, especially at Timberline, where, of course, it thrives. Great difficulty has been experienced in establishing it in the gardens at Stanford, because it dies out repeatedly and shows very little growth. At best the propagules usually live but a year or two, and few or no flowering stems are produced. At Mather, on the other hand, the species grows with magnificent vigor, forming extensive matlike colonies from which an abundance of stems develop. The modifications one observes at the three altitudinal stations are not at all impressive, as shown in figure 146. At Stanford, as compared with Mather, the few stems produced are very short, the leaves are reduced in size, and they are usually thicker. The greatest size and

vigor is attained at Mather, for although the species thrives at Timberline, its growth is relatively limited. When *multiradiata* is brought into cultivation at Timberline, it is but little modified as compared with its appearance in the wild, as is shown in figure 146.

Solidago multiradiata flowers much earlier than the mid-Sierran *S. elongata*, as is shown in figure 148. Figure 147 shows the lengths of the flowering stems, and figure 153 the survival records of these two species at the three transplant stations, along with similar data for the races of *Aster adscendens*, to be discussed in later paragraphs.

The following tabulation of Mather reactions shows the differences between the two species in three characters, the relative constancy of each population, and the remarkable number of stems produced by the alpine *multiradiata* at this relatively low elevation. The averages given are computed from data from 1935 to 1937.

Plant number and origin	Longest stems (cm.)	Number of stems	Date of first flowers
<i>Solidago elongata</i> :			
from Mather, 1400 m.			
1310-1.....	101.3	88.3	July 1.7
-2.....	101.7	105.0	June 29.7
-3.....	100.7	90.0	June 28.7
<i>S. multiradiata</i> :			
from Tioga Pass, 3030 m.			
1311-1.....	23.0	43.7	May 25.0
-2.....	20.3	70.0	May 19.7
-3.....	20.3	29.7	May 24.0
-4.....	27.0	100.0	May 19.7
-5.....	25.5	66.7	May 27.5

The plants of *multiradiata* had all been in the Mather environment continuously for ten years, but none of them approaches the native *elongata* in either height or earliness, or in the characters of its inflorescence, as seen in figure 146. The relative stability of the Sierran *multiradiata* in very different environments and over a long period is at variance with the reported flexibility of the Colorado form of the same species (Clements, 1934), which is stated to have changed into the species of the plains, *S. missouriensis*, after being transplanted into the environment of that species. A change of the Tioga Pass form into the Mather species would have been of the same general order.

From the studies with these two species of *Solidago* it is clear that *elongata* is obviously better fitted to the mid-Sierran climate than to



FIG. 146. Modifications in a clone of alpine *Solidago multiradiata* at three altitudes.

This plant, 1311-5, was dug September 13, 1926, in Tioga Pass, at 3030 m. The propagules were planted at Stanford in 1935 (from a Mather division), at Mather in 1927, and at Timberline in 1933. The specimens were taken at Stanford and Mather in 1937, and at Timberline in 1935.

either that at Stanford or at Timberline, whereas *multiradiata* is equally successful at both of the mountain stations.

Both species are diploid, as determined on the following plants:

Solidago elongata Nutt., $n=9$:

1310-3, Mather, Tuolumne Co., 1400 m., in roots.

Solidago multiradiata Ait., alpine forms, $n=9$:

1311-5, Tioga Pass, Mono Co., 3030 m., in roots.

Clausen F.5115, Slate Creek Valley, Mono Co., 3050 m., meiotic in pollen mother cells.

This is in agreement with previous counts by various authors, who have found five diploid species, $n=9$, one tetraploid, $n=18$, and one hexaploid, $n=27$, namely, *Solidago nemoralis* Ait.

No crossings have been attempted between these two Sierran species, but there are indications that morphologically very distinct *Solidago* species may be genetically closely related. Goodwin (1937a, 1937b) produced hybrids between the diploid species *S. rugosa* Mill. and *S. sempervirens* L. They differ in inflorescences and leaf margins in a manner similar to *S. elongata* and *S. multiradiata*, and occupy ecologically different habitats. The hybrid is highly fertile

and is found in the wild where the two species meet. A tendency for the natural hybrids to be attacked by leaf-eating insects, and for the artificial ones to be attacked by rust, were the only indications of

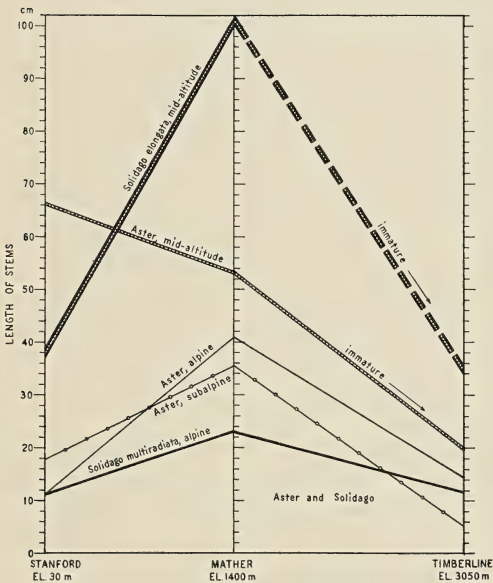


FIG. 147

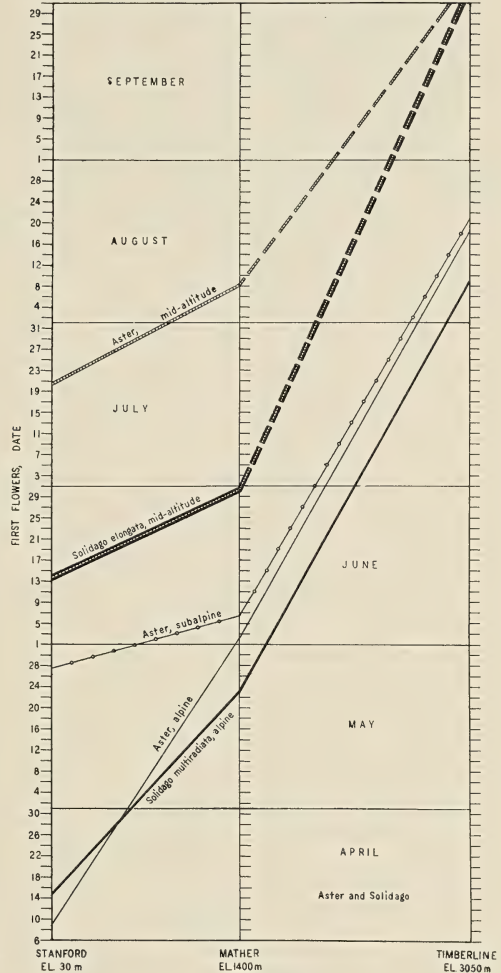


FIG. 148

Modifications at three altitudes in length of stems (fig. 147) and earliness (fig. 148) in clones representing ecotypes and ecospecies of *Solidago* and the *Aster* *adscendens* complex.

The graphs represent averages from the years 1934 to 1937 for the plants listed in figure 153.

slight constitutional weakness. Studies of natural populations indicated that some exchange of genes takes place where the two species meet. They cannot, therefore, be more than very closely related ecospecies in spite of their marked morphological differences.

THE ASTER ADSCENDENS COMPLEX

The Asters related to *Aster adscendens* Lindl. are frequent occupants of meadows in the Sierra Nevada and grow at altitudes ranging from 1000 to 3200 m. They extend from California to Colorado and Saskatchewan. The Sierran forms in our cultures, shown in figures 149 to 152, were identified by Dr. S. F. Blake, of the Bureau of Plant Industry, as *A. occidentalis* DC. The series has not been thoroughly studied in the field, particularly as to the occurrence of intermediate forms, but it is evident that the group represents another case of differentiation into ecotypes and ecospecies suited to a wide range of climatic conditions.

The marked differences between races from contrasting altitudes along our Sierran transect are illustrated in figure 149. The mid-Sierran, subalpine, and alpine forms all have the same number of chromosomes ($n=16$), while the Great Basin form, which is probably a distinct but related species, has half as many ($n=8$).

The reactions of the mid-Sierran, subalpine, and alpine forms at the three transplant stations are shown in figures 150 and 151. The mid-Sierran race (fig. 150, 1306-1) shows relatively minor differences between Stanford and Mather, and, because of its slow seasonal development, it produces only immature shoots at Timberline. Striking modifications are shown by the alpine and subalpine races (fig. 151), whose stature is greatly influenced by the environment, as one can see by making the horizontal comparisons. At Stanford, as compared with Mather, both are much dwarfed in size, especially the alpine (fig. 151, 1306-22); at Timberline, too, they are much reduced in stature, but it is the subalpine (1306-11) that is reduced the most.

The differences between the altitudinal ecotypes are most striking when the three are grown in a uniform garden at Stanford; there the mid-Sierran is the tallest, the alpine the dwarfiest, and the subalpine is intermediate (cf. also fig. 149). At Mather the subalpine and alpine look much alike, although a careful observer would see differences. A visitor to the gardens at Timberline would get still another impression of the three, and might even mistake the alpine modification of the subalpine race for another species, *A. Andersonii* Gray, which is common around Timberline, although a close study of its characters would make evident this error.

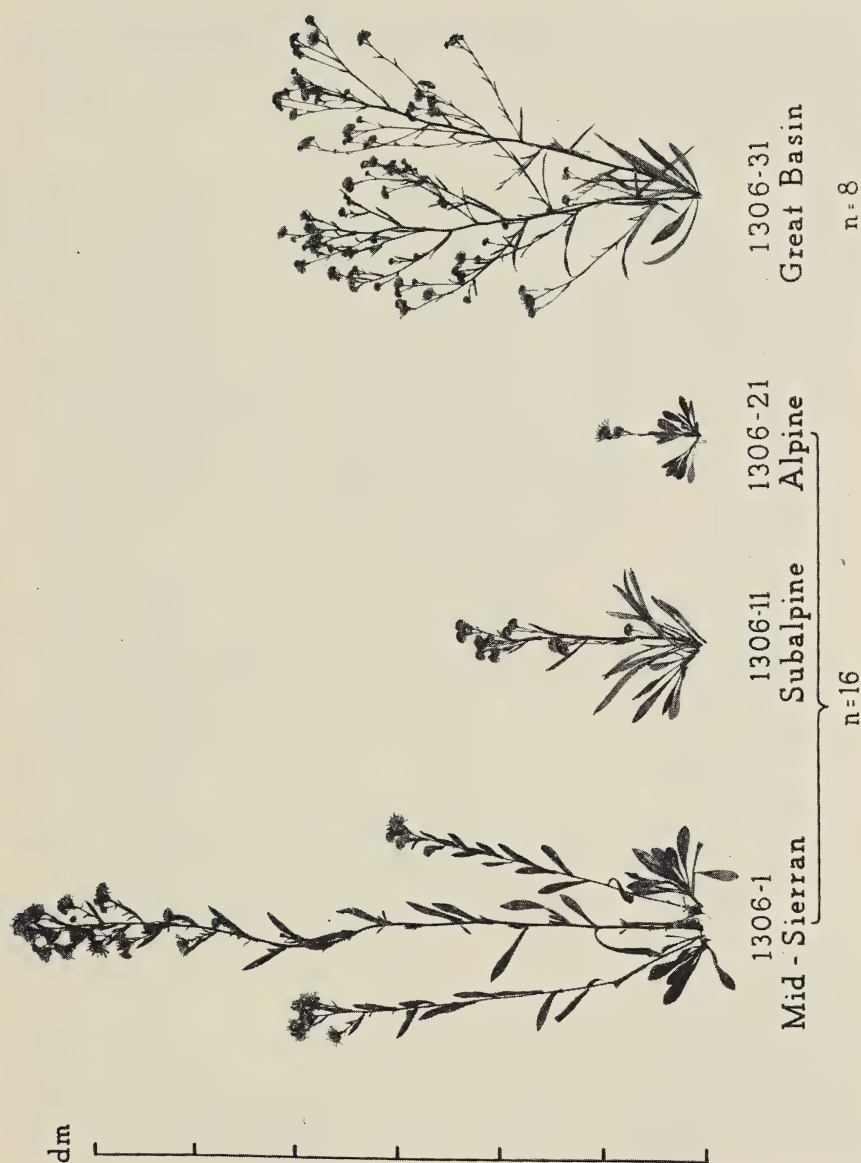


FIG. 149. Forms representing altitudinal races and species of the *Aster adscendens* complex in California grown at Stanford.

1306-1, from Mather at 1400 m.; 1306-11, from Tuolumne Meadows, Yosemite Park, at 2700 m.; 1306-21, from near Timberline station at 3050 m.; and 1306-31, from near Mono Lake, Mono County, at 2070 m.

The three altitudinal races differ also in their seasonal rhythms at the transplant stations. The alpine and subalpine forms are essentially evergreen at Stanford, but develop more leaves in spring than at any other time. The alpine blooms early (fig. 148) but sparingly—a characteristic already noted in alpine species when grown at Stanford. The subalpine plant, as compared with



FIG. 150. Modifications in a clone of mid-Sierran *Aster ascendens* at three altitudes; $n=16$. This plant, 1306-1, was dug September 27, 1925, near Mather. The propagules were planted at Stanford in 1929 (previously at Berkeley 1926-1929), and at Mather and Timberline in 1934. Specimens taken in 1935.

the alpine, is delayed about forty-five days at Stanford, but not at Mather. After flowering, their rosettes continue to grow slowly, but during the late summer and fall they suffer somewhat from attacks by rust and red spider, and from drought. While flowering stems are usually produced in early spring, sometimes additional ones are developed later in the season. These later stems are usually taller than those of early spring, as is shown by the specimens of the subalpine race at Stanford in figure 151 taken in May and August.

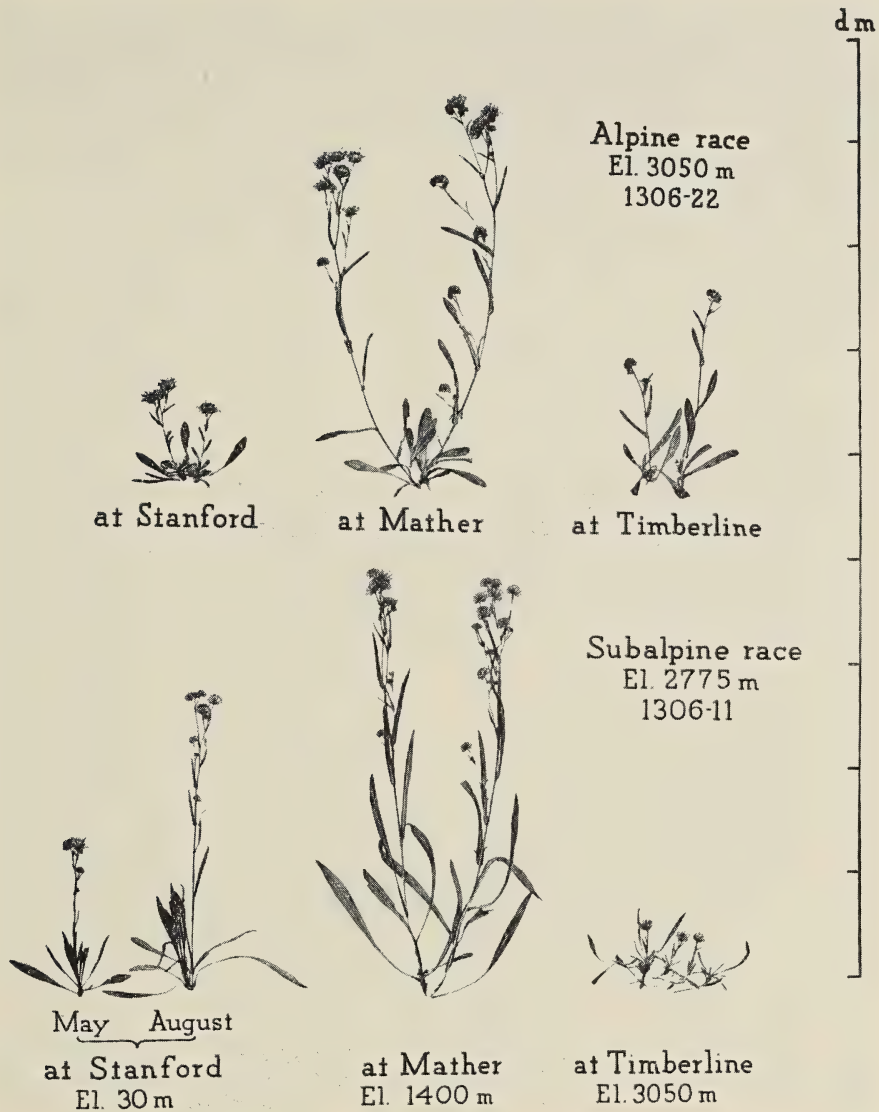


FIG. 151. Modifications at three altitudes in clones of alpine and subalpine *Aster adscendens*; $n=16$.

The alpine plant 1306-22 is from near Timberline station; its propagules were planted in 1934, and the specimens taken in 1935. The subalpine plant 1306-11 is from Tuolumne Meadows; the propagules at Stanford and Mather were planted in 1934 as divisions from the one at Timberline, which was set in 1929. The specimens were taken from Stanford in 1937, from Mather in 1935, and from Timberline in 1932.

At Mather all three altitudinal ecotypes are dormant in winter and begin spring growth in April. The alpine is first to flower, and is soon followed by the subalpine (fig. 148). The mid-Sierran lags at least two months behind at Mather and even more at Stanford. At Timberline, it is far too slow to reach flowering, whereas the other two races succeed fairly well in ripening seed, although the subalpine does not bloom there nearly as consistently as the alpine.

Modifications produced by growing clone members in a series of contrasting environments at one station, as in the water-light gardens at Mather, are shown in figure 152. The mid-Sierran form (1306-1) varies considerably in stature and in size of leaves. For some reason difficult to explain, the clone member in the moist sun garden is conspicuously shorter-stemmed and smaller-leaved than the others, and this difference was consistent year after year. Sun and shade alone seem to have less relative effect by themselves, but the two variables in the right combination evidently influence growth quite strikingly. The subalpine is but little modified in this series of gardens, but it produces visibly wider leaves in shade than in sun. The modifications in the water-light gardens do not compare in magnitude with those brought about by transplanting to different altitudes, as shown in figures 150 to 152.

The lengths of stems at the three transplant stations for the various races of *Aster adscendens* and the two species of *Solidago* discussed above were shown in figure 147. The mid-altitude *Aster* produces longer stems at Stanford than in its native environment at Mather. This is similar to the reactions of *Achillea* and *Artemisia*. The survival graph, figure 153, is a record of some of the individuals of both *Solidago* and *Aster*, and indicates in some detail the success of the various transplants at the different altitudes.

The three altitudinal forms are characteristic representatives of the natural populations. The differences between them are so great that they indicate that this Sierran *Aster* is a species differentiated into altitudinal ecotypes having very different potentialities for development in unlike environments. It is obvious that their physiological properties differ so as to fit them to the habitats in which we find them growing as natives.

The cytological survey of this group has been confined to the individuals used as transplants. The forms from the Sierras were all tetraploid, $n=16$, irrespective of their great morphological differ-



FIG. 152. Modifications in clones of subalpine and mid-altitude *Aster adscendens* in the water-light gardens at Mather.

The subalpine plant 1306-11 is from Tuolumne Meadows at 2700 m.; its propagules were planted in 1934, and the specimens taken in 1937. The mid-altitude individual 1306-1 is from Mather at 1400 m. Its propagules in the dry sun and moist shade were planted in 1937, the others in 1933; the specimens were taken in 1936.

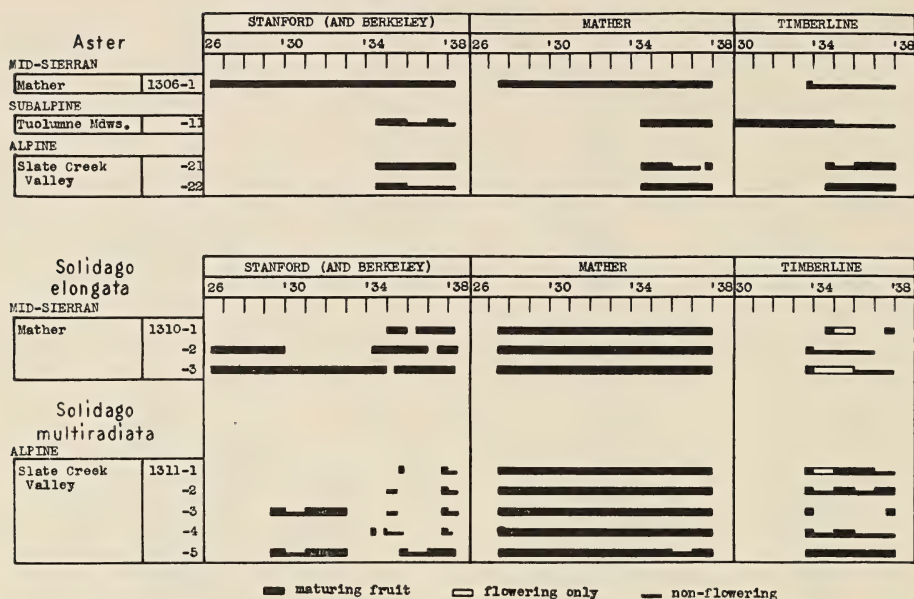


FIG. 153. Record of survival and flowering of clones representing different forms of *Solidago* and the *Aster adscendens* complex at three transplant stations. See text. The scale indicates years.

ences as seen in figure 149. However, two plants from the Great Basin, only some 30 km. removed from the alpine 1306-21, but at an elevation 1000 m. lower, were diploid, $n=8$. The diploid plants developed a much more expanded inflorescence at Stanford (fig. 149). In the tetraploid forms there is a slight tendency for quadrivalent association of chromosomes, and chromatin bridges are observed. The details of the chromosome determinations are listed below. All except the last one were determined in meiosis of pollen mother cells.

ASTER ADSCENDENS COMPLEX

Sierran species, tetraploid, $n=16$:

1306-1, Mather, Tuolumne Co., 1400 m.; usually one quadrivalent; also occasional chromatin bridges in first anaphase that sometimes remain to second metaphase; a lost chromosome or fragment of a chromosome is often seen in the cytoplasm of pollen mother cells.

1306-11, Tuolumne Meadows, Yosemite Park, 2650 m.; meiosis is more regular than in the preceding plant, but six out of twenty-five pollen mother cells showed a lagging and dividing chromosome in first anaphase; the tetrad groups of young pollen sometimes include a fifth very dwarf grain, probably formed around a single detached chromosome.

1306-22, Slate Creek Valley, Mono Co., 3050 m., a plant similar to 1306-21 in figure 149. Meiosis is quite regular, although an occasional quadrivalent is seen.

Great Basin species, diploid, $n=8$:

1306-31, near Leevining, Mono Co., 2070 m.; 8 pairs plus one very small fragment seen regularly in first metaphase; the fragment does not appear to divide, but arranges itself in the equatorial plane at the margin of the group of bivalents. Its later fate is unknown.

Hiesey 347-2, from the same locality; somatic mitoses in the floral region.

A Eurasiatic group of seven species of *Aster* following a 9 series ($n=9, 18, 27$) was discovered by Tahara and Shimotomai (1926). Two species of the eastern United States, *A. novae-angliae* L. and *A. multiflorus* Ait., have $n=5$ (Carano, 1921; Morinaga and Fukushima, 1931; Delisle, 1937). The present two species, which follow an 8 series, are of a west American group. Such differences in basic chromosome number often prove to be of great help in determining relationships of taxonomically difficult groups, especially when the differences are correlated with geographical distribution. We are not prepared, however, to offer any theory on the phylogeny or relationships of members of the complex genus *Aster*. Many more chromosome counts, extensive hybridization work, and a study of the reactions of many series of plants in uniform and in varied environments should yield much of interest in this genus.

XI

REVIEW OF LITERATURE

Few scientific investigations have been made on the effect of transplanting closely allied forms of higher plants to different climates. The most extensive of such experiments are those of Kerner (1891), Bonnier (1889–1920), MacDougal (1921), and Clements (1929). The work of Turesson (1922*a*, 1922*b*, 1925) in bringing different forms of the same species into a uniform environment has added much to our understanding of the relationships between plants and their surroundings, as will be seen in more detail later. Much supplementary evidence has been amassed by other workers.

KERNER

Within the pages of his monumental *Pflanzenleben*, A. Kerner von Marilaun (1891, vol. 2, pp. 489–507) describes what are probably the first scientific transplant experiments of the varied-environment type. He developed an alpine garden in the Tyrolean Alps at 2195 m. elevation, and another near his villa at Marilaun in the same mountains at 1215 m., utilizing as lowland stations the botanic gardens at Innsbruck (elevation 569 m.) and at Vienna University (elevation 180 m.). These studies involved both annual and perennial plants.

The annuals included species of the lowlands which were sown both at Vienna and at the alpine garden. Among these were *Agrostemma Githago*, *Centaurea Cyanus*, *Iberis amara*, *Lepidium sativum*, *Satureia hortensis*, *Senecio vulgaris*, *Turgenia latifolia*, *Veronica polita*, and *Viola arvensis*. Some species were killed at the high altitude by frosts, others resisted the cold but developed only vegetative rosettes because of the short growing season, a few produced inflorescences, and a very limited number were capable of maturing ripe seeds. Kerner took herbarium specimens of plants grown in his alpine garden and compared them with specimens of the same species at Vienna. He found that the annuals which flowered at the high altitude had shorter stems and internodes, fewer nodes, and fewer and often smaller flowers than those grown at Vienna. Only *Senecio vulgaris*, *Veronica polita*, and *Viola arvensis* produced ripe fruit at the alpine garden. Certain annuals, which did not flower at the high

altitude because of the short season, tended to survive the winter and produced new shoots the following spring, sometimes even continuing to live several seasons. These included *Poa annua*, *Senecio nebrodensis*, *S. vulgaris*, *Ajuga Chamaepestis*, *Herniaria glabra*, *Viola tricolor*, *Cardamine hirsuta*, and *Medicago lupulina*.

Kerner experimented with over three hundred perennial species, growing similar batches of seed of a given species in his alpine experimental garden on the Blaser and at Vienna or Innsbruck. Only thirty-two of these species succeeded in coming into flower at the high elevations during the six years in which he carried on his experiments. Those which flowered reacted much like the annuals: flowering stems and internodes were shorter, nodes fewer, leaves smaller, and flowers fewer and often smaller than on corresponding plants of the same species at the lowland station. As an example, Kerner reported results from *Lychnis Viscaria* (*op. cit.*, p. 502) as follows:

Character	Vienna (elev. 180 m.)	Alpine garden (elev. 2195 m.)
Height of stem, including inflorescence	400-450 mm.	230-240 mm.
Size of lower leaves	80 × 4 mm.	50 × 3 mm.
Size of inflorescences	80 × 50 mm.	60 × 40 mm.
Calyx	15 × 6.5 mm.	13.5 × 5 mm.
Petals	10 × 8 mm.	8 × 6.8 mm.
Claw of petals	8 mm.	7 mm.
No. internodes	9	6-7
No. flowers per cyme	3-5	3
No. flowers per inflorescence	33-40	5-11

The plants in Kerner's alpine garden developed more pronounced red and yellow pigmentation in flowers and in vegetative parts than did those at Innsbruck or Vienna. On the other hand, green tissues were not of as dark a shade at high as at low elevations. Kerner ascribed these modifications in color to the differences in intensity of light at the two altitudes, and supposed that the strong light of high altitudes decomposed chlorophyll, but favored the synthesis of anthocyanin and xanthophyll. Species growing naturally in shade or semi-shaded habitats at low elevations, such as *Arabis procurrents*, *Digitalis ochroleuca*, *Geum urbanum*, and *Valeriana Phu* developed more or less yellowish leaves in the alpine garden.

Kerner carefully distinguished between hereditary differences and temporary modifications. He regarded modifications as advantageous adjustments to changed environments, and held that the capac-

ity for adaptation is founded upon the specific constitution of the protoplasm. Although Kerner did not deny the possibility of modifications' becoming hereditary, he produced evidence against this hypothesis. He gathered seeds from transplants grown at the alpine station and at Marilaun, which had shown distinct modifications when compared with plants of the same species at Vienna, and grew them beside seedlings of his Vienna transplants. In no instance were the modifications of the parents transmitted to the offspring.

These experiments, among others, led Kerner (*op. cit.*, p. 506) to conclude: "Die Anpassung bewegt sich bei jeder Art innerhalb bestimmter Grenzen, welche in der spezifischen Konstitution des Protoplasmas begründet sind und nicht überschritten werden können." Thus, Kerner reached the same conclusion fifty years ago that we draw from our experiments today. Kerner's transplant studies have largely been given only passing mention by botanists who succeeded him, the more spectacular but less discerning work of Bonnier having appealed more to writers of textbooks in botany.

BONNIER

The transplant experiments of Gaston Bonnier have been considered by many to be classic. In view of this author's striking conclusions and their biological implications, we shall consider his work in some detail, especially since our findings are in fundamental disagreement with his.

METHODS. Bonnier introduced the method of clone transplanting. In general, he endeavored as far as possible to take an individual native of an intermediate elevation, divide it into two parts, and plant one half at a low altitude, and the other at an alpine station. In some cases he used seeds. These were harvested from the same individual for a given experiment, those to be sown at low and at high altitudes being divided into equal packets. In order to eliminate the influence of the soil, Bonnier transported it from the high stations to the lower.

Bonnier did not cultivate, weed, irrigate, or apply fertilizer to his plants, subjecting them to the competition of native vegetation and hence to "natural" conditions. He attempted, rather unsuccessfully, to protect his cultures in the mountains against grazing animals by fences, and finally resorted to planting them in inaccessible places,

such as on sharp declivities and in rocky crevices where they were not easily reached. He marked their position by such means as carvings on rocks and stakes. Thus, the clone members of Bonnier's plants in the montane environment were subjected to rugged vicissitudes of existence comparable with those of native wild species.

During the years 1886 to 1889, 100 cultures were established in the Pyrenees, and in 1887 and 1888, 103 more were set in the Alps, base stations at Paris, Fontainebleau, Pierrefonds, and Mirande (in Gers) serving as termini for the transplants in both mountain ranges. The great bulk of Bonnier's published experimental evidence was obtained from these 203 cultures. He recorded his observations in the form of notes, which seem to have been his chief means of study. He apparently did not take herbarium specimens from his plants systematically, since no preserved materials of his experiments are available for present-day reference except his published illustrations. Bonnier made anatomical as well as gross morphological studies, and also described physiological experiments on his transplants, attempting to compare rates of transpiration, respiration, and photosynthesis.

RESULTS. Bonnier summarized his observations and conclusions in three memoirs (1890, 1895, 1920); in addition to these, he published numerous smaller papers. His review of 1890 includes a description of his methods, and an account of the gross morphological differences observed up to that time. In 1895 Bonnier surveyed the anatomical as well as the morphological changes induced, reported on his physiological experiments, and concluded that the changes he observed following transplanting were due principally to differences in light, temperature, and humidity. In his final publication of 1920 Bonnier reported on observations made on his original cultures thirty to thirty-five years after transplanting, and there presented his most spectacular results and far-reaching conclusions.

He reported that a great many species brought from low to high elevations had been transformed from lowland into alpine forms, and cited examples where varieties or species previously considered to be distinct became alike. For example, after thirty years at 2400 m. elevation, plants of *Helianthemum vulgare* Gaertn., originally from the lowlands, became like *H. grandiflorum* DC.; *Polygala vulgaris* L., grown for twenty-five years at 1800 m., changed to *Polygala alpestris* Rechb.; *Silene nutans* L., grown for thirty-four years at 2300 m.,

was transformed into *S. spathulaefolia* Jord., while *S. inflata* Sm., which resembled *S. alpina* Thomas after six years at an alpine station, became much more like the latter species twenty years later. *Lotus corniculatus* L. was modified considerably at the end of ten years, but on longer exposure at high altitudes it became identical with *L. alpinus* Schleich., while *Solidago Virgaurea* L. was quite promptly transformed into *S. alpestris* W. & K. He wrote (1920, p. 308): "Parmi les plantes de mes cultures, on peut citer comme ayant ainsi réalisé une adaptation non pas seulement 'dans le même sens' que celle qu'on observe chez les végétaux similaires naturellement alpins, mais une adaptation morphologique et anatomique *absolument complète* en trente ou trente-cinq ans, ceux appartenant aux espèces suivantes:"—following which he listed fifty-eight species in which conversions from one taxonomic variety or subspecies into another were effected by transplanting.

Certain limitations, however, were emphasized by Bonnier in the capacity of plants of one altitude to adapt themselves to another. In the first place, he found that it was impossible successfully to adapt any plant to another climate where forms of the same or of a related species did not grow naturally. When lowland plants were set amid alpine forms, the former became adapted and eventually exactly like the latter; but when placed in an altitude above the upper limits of occurrence of the alpine forms, they eventually succumbed to the elements, meanwhile failing to develop any of the morphological qualities of alpine forms.

In the second place, Bonnier found it difficult to make the reverse change, that is, the transformation of alpine into lowland forms, although he cites a few examples where, within quite restricted altitudinal limits, such adaptations took place. He explained the frequent failure of plants from alpine regions to become tall like the true lowland forms as follows: the alpiners were brought to an elevation below the natural limits of the range of the species, and hence were unable to adapt themselves and become lowland forms. The common observation of horticulturists that alpine plants cultivated in lowland gardens retain their original characters was thus accounted for. Such alpiners in lowland gardens owe their continued existence solely to cultivation—an artificial situation, for, according to Bonnier, such plants, being below their natural range of altitude, would soon perish in competition with lowland species.

BONNIER'S CONCEPT OF SPECIES. Bonnier developed a unique hypothesis concerning the distribution of a species across a range of altitudes. He conceived of a species (in its broadest Linnaean sense) as a unit, the members of which have a more or less extensive capacity for adaptation to different environments. Thus, the altitudinal range covered by a species represents its ability to accommodate itself to a range of climates, and the differences between forms at different elevations are merely adaptations of the same basic thing, i.e., the species. Somewhere within its range, each species has an optimum altitude at which it develops best. This, according to Bonnier, can be determined approximately by field observation, for at its optimum the species has the darkest green leaves, the highest degree of tissue development, and the deepest tones of flower color. Above the optimum, foliage becomes less intensely green, flowers lose some of their color, and plants have less and less ability to adapt themselves through structural changes as higher altitudes are reached, until finally the upper limit of survival is encountered. Likewise, plants brought below their optimum show similar effects, so that at the lowest altitudes they can survive only when nursed along in gardens with much care, and lose all capacity for adaptation.

That Bonnier encountered inconsistencies between this hypothesis and facts which he observed is evident in his 1895 report (pp. 320-326), where he describes his attempts to correlate the anatomy of different forms of the same or related species, and of different species of the same genus, with altitude, in *Thalictrum*, *Lotus*, and *Saxifraga*. He observed that there was a great complexity of structure within plants from many habitats. From this he concluded that many factors operate to produce morphological diversity, climate being but one factor. However, in using clone members of the same individuals transplanted to different altitudes, he supposed he was able to study the "sole effect" of climate.

DISCUSSION OF BONNIER'S RESULTS. Bonnier was probably led to wrong conclusions through errors in his methods. His use of clone members was commendable, but unfortunately his only record of observations was apparently in the form of notes. He took no herbarium specimens through which others might verify his results. Moreover, inasmuch as he did not weed or cultivate his transplants after they were set out, and as he permitted them to remain in vari-

ous places in the mountains for years without care, it is very likely that at least some of his cultures became contaminated. Thus two sources of error were probably involved: first, the inexact comparison of plants before and after transplanting, and second, contaminations in his cultures.

Both of these sources of error are easily comprehended in the light of our experience with transplanting. It has already been pointed out (p. 23) that the interpretation of a body of data collected from experiments in which results are expressed in terms of quantitative characters is difficult. This is especially true because modifications frequently simulate hereditary differences. Only after a period of years, when a series of herbarium specimens has been accumulated from each clone member, can one satisfactorily compare the effect of a difference in climate upon the propagules of the same individual. No system of note-taking, however complete, can describe accurately all the details of structure; therefore Bonnier was obviously handicapped through his dependence upon notes alone. In our experience, even measurements of heights, sizes of leaves, etc., are valuable only when extensive enough to be regarded statistically, and when supplemented by herbarium material.

One of the most difficult problems in the transplant experiments has been to keep the cultures pure. We have found that much laborious effort is required to destroy seedlings that germinate near or under a transplant, and to root out rhizomes which may invade it from near-by plants. Seedlings may originate from the transplant itself or from neighboring plants. In either case, they are not identical with the original clone in genetic constitution, and if allowed to persist may be mistaken for the original. Even in well-cultivated gardens it is necessary to be constantly on the search for such intruders. As plants become older and their bulk increases, this task becomes increasingly difficult. In Hall's experience with "reciprocal transplants," he soon discovered that contamination was practically certain after two or more years under "natural" conditions unless rigorous elimination of interlopers was practiced. We can scarcely conceive of transplants growing under natural conditions without cultivation for any length of time without at least a certain percentage of contamination.

It is significant that Bonnier's most spectacular transformations

were reported in 1920, thirty to thirty-five years after his experiments were started. It is probable that very few, if any, of his original plants lived for such a long period. They were most likely replaced by natives which became so well established that they were mistaken for the original transplants. In this connection, it is significant that Bonnier reported transformations from lowland into alpine plants only when they were brought to a region where related forms of the same species were growing; moreover, such "transformed" lowland plants were always *exactly* like the alpine natives!

These criticisms of Bonnier are made in the hope that a repetition of his work, using the same species in the same region under carefully controlled conditions, may be stimulated. As the attention of botanists is becoming more and more directed to a study of smaller races within the species and their possible rôle in evolution, more precise knowledge of their reactions to different habitats becomes highly desirable, for such studies are needed for further clarification of our knowledge of the relation between plants and their environment.

MACDOUGAL

In a study of a rather general nature, D. T. MacDougal (1921) attempted to determine the factors involved in the dissemination, establishment, and adaptation of plants to new environments. This involved growing corresponding sets of 139 different species under four different climates: (1) near the Pacific Coast at Carmel, California, (2) at the Desert Laboratory of the Carnegie Institution at Tucson, Arizona (elevation 700 m.), (3) at a xeromontane station in the Santa Catalina Mountains near Tucson at 1585 m. altitude, and (4) at a high-montane station on Mount Lemmon in the same range at 2440 m. The cultures were grown from seeds, tubers, corms, rhizomes, or shoots at these different stations and, after they had been allowed to struggle with the elements ten to fourteen years, their survival and dissemination were noted. The published data contribute very little to our knowledge of the capacity of given species to become modified at different environments, for the results were interpreted more on the basis of the mode of propagation of plants and their survival capacity in different kinds of environment than from the viewpoint of modification.

CLEMENTS

F. E. Clements (1918–1938) has published brief references to his extensive experiments conducted along a transect at Pikes Peak, Colorado, and at Santa Barbara, California. General claims of transformation of lowland into alpine forms and vice versa have been made (cf. Clements, 1929). The character of the transformations and the circumstances under which they arise are essentially the same as those claimed by Bonnier. Examples of the very numerous conversions reported by Clements are *Erigeron salsuginosus* into *E. uniflorus*, the subalpine *Solidago Virgaurea multiradiata* into *S. missouriensis* of the plains (1934), *Epilobium angustifolium* into *E. latifolium* (1926), repeated conversions of *Phleum pratense* into *P. alpinum* (1925, 1926), and the reciprocal conversion *Phleum alpinum* into *P. pratense* (1933). (In this connection it is well to remember that the two *Phleum* species differ in their number of chromosomes.) Inasmuch as no well-documented reports have as yet been published on these experiments, it is obviously impossible properly to evaluate these claims.

TURESSON

The investigations of Göte Turesson are of great significance in clarifying the relation between polymorphic forms of a species and their environment. His methods differed from those of Kerner and Bonnier, in that instead of bringing plants to diverse climates, he assembled forms from different climates in a uniform garden. This collection of forms was grown at the Institute of Genetics at Åkarp, Sweden. Species having a wide and continuous geographical distribution over a variety of climates were especially selected for study, materials having been collected from different places in Sweden, Norway, the Faeröes, England, Scotland, Denmark, Germany, Austria, Italy, Russia, and Siberia.

Turesson included samples of twenty or more individuals in each collection, to secure possible variants within a given population. He also utilized seedlings from transplanted individuals which were isolated in groups of two, to induce mutual pollination for the propagation of the races. These seedlings retained the general characteristics of the population from which they originated. By comparing such collections in a standard environment and performing genetic experiments upon them, he obtained a unique and illuminating mass

of data demonstrating the existence of many hereditary forms within a number of species.

Turesson emphasized the physiological characters, such as time of flowering (earliness), as most important indicators of the ecotype. He found that, in general, southern European, alpine, and high nordic ecotypes were the earliest, and that lowland forms from northern and central Europe were the latest when grown in the Åkarp standard environment. He has also demonstrated that certain morphological types tend to be associated with particular habitats; for example, alpine forms in general are dwarf, and lowland types tall, while maritime plants often are characterized by a prostrate habit and thick, fleshy leaves. Forms from lower latitudes are as a rule taller than plants from the far north, which resemble the alpiners in height. On the basis of his experimental results, Turesson proposed a classification of plants into *cenospecies*, *ecospecies*, and *ecotypes*, a system adopted in essentials by the writers (1939).

Turesson described modifications resulting from the transfer of plants from their native habitats into cultivation, especially when these were taken from exposed places. Thus, alpine forms in general became taller, and prostrate maritime plants would sometimes become erect in his protected experimental garden. Turesson emphasized the fact that modifications sometimes may parallel genetic differences.

The principles established by Turesson relating to species composition and the association of given hereditary types in certain kinds of habitats apply very well to species in California that have been included in our transplant experiments.

OTHER INVESTIGATORS

Alexis Jordan (1846, 1864, 1873) took hundreds of strains of complex plant groups into culture in southern France. In such groups as the violets and the *Erophila verna* complex, he proved the existence of many hereditary forms that remained distinct in a uniform environment. Jordan considered each such constant race to be a species, and thereby incited much discussion concerning the nature of species. Using the same approach, later botanists realized that this concept would create confusion, so they considered such races to be elementary species or microspecies. In recent years Turesson has focused

attention on the ecological importance of many of these races, and his findings have been confirmed by many other investigators during the past fifteen years.

A clear demonstration of the interaction of environmental and hereditary differences upon the phenotypical expression of *Plantago maritima* is furnished by J. W. Gregor and his associates (1930, 1936). Just as Turesson pointed out the parallelism between modifications and genetic characters in *Succisa pratensis*, *Centaurea jacea*, and other species, Gregor has found this to be true in localized populations of *Plantago maritima*.

Gregor and Sansome (1927) have produced similar evidence in *Lolium perenne* L., *Dactylis glomerata* L., *Phleum pratense* L., and *P. alpinum* L. Plants of these species removed from their natural habitats to experimental gardens at Edinburgh have shown that definite hereditary races occur within these groups, and that genetic types are clearly differentiated from modifications, although the latter may simulate the former.

Closely allied to these facts are the findings of Stapledon (1928) in studies made on *Dactylis glomerata* L. This author reports upon investigations made at the Welsh Plant Breeding Station with 143 collections from seed obtained from countries in different parts of the world, and on 315 individual turfs dug in England, Scotland, and Wales. After eight years of critical breeding studies, cultures having been carried up to the fourth generation, this author concludes that *D. glomerata* shows marked habitat relationships which are genetic in nature.

Under the auspices of the British Ecological Society, Marsden-Jones and Turrill (1929, 1933, 1935, 1937, 1938), at Potterne, Wiltshire, England, have conducted experiments on the influence of varied soils on a few selected species. These included a sand, a calcareous sand, a clay, a chalky clay, and a soil from Potterne, each of which was placed in a large wooden bin. *Centaurea nemoralis* Jord., *Silene vulgaris* Garcke, *S. maritima* L., *Anthyllis vulneraria* L., *Plantago major* L., *Fragaria vesca* L., *Phleum pratense* L., and *P. nodosum* L. were included in the cultures. The authors found only relatively slight modifications, although the species varied in their response to the soil differences. The range and kind of plasticity were found to be as inherent as morphological characteristics. This agrees with our observations.

Aquatic and amphibian plants have long been known to produce very different stem and leaf structures in different habitats, particularly in species adapted both to a terrestrial and to an aquatic mode of growth. A vivid account of experimentally demonstrated modifications in *Polygonum amphibium* L. was given by Jean Massart (1902). Three morphologically different forms of this species are known: (1) a "normal" terrestrial form in wet soils along the water's edge; its stems are erect and swollen above the nodes, and the leaves are lanceolate and pubescent on both surfaces; (2) an aquatic form, whose internodes are slender and elongated, the stems more or less horizontal, while the long-petioled floating leaves are acuminate at the base and glabrous; and (3) a xerophytic form with prostrate branches, very short internodes, and very thick, pubescent leaves.

Massart transplanted the terrestrial and dune forms to dry sand, moist sand, and water, and obtained the modifications expected according to the habitat, but he did not transplant the aquatic form. Although Massart's experiments showed that the terrestrial and dune forms could be modified into forms that morphologically corresponded to the others, he did not show that they were genetically identical. However, he rightly emphasized the difference between hereditary differences and modifications, and pointed out that amphibious plants such as *Alisma*, *Stratiotes*, *Ranunculus aquaticus*, and *Veronica anagallis* were much more widely adaptable, both in morphology and in their capacity to occupy diverse habitats, than average terrestrial plants or than strict aquatics such as *Chara*.

An experiment whereby parts of pure lines were exposed to different climates for ten generations in a ten-year period was reported by Christie and Gran (1926). Seven strains of oats and two of barley were sown at six experiment stations in Norway ranging from 58° 51' to 65° 50' N. Some of these stations were on the humid coastal side of the country, others on the drier continental side. Reactional differences between the strains were observed at the stations during these years. The reactions listed include: time required for germination and maturation, and the length, width, and number of straws produced.

The various strains were modified to some extent at all stations, but they tended to keep their relative positions in earliness, and in length and width of straws. The tallest plants were produced at the

southern coastal and the northernmost station. The most rapid maturation took place at the most continental station in the south, and the slowest at the southernmost coastal station, where the longest straws were produced. After ten years, when the strains were all brought back to a seventh central station for comparison, there was no effect of the differential influences they had been under for ten generations.

Evans (1939) reported a study involving the planting of clone members of ten early to late races of timothy, *Phleum pratense*, at ten stations located over a range of 28° of latitude, from Gainesville, Florida, to Fort Vermilion, Alberta. Interesting modifications in morphological characters and in relative earliness were reported. At Washington, D. C., at $38^{\circ} 9' N.$, the ten varieties tested varied in the appearance of their first florets in 1935 between June 3 for the earliest variety and August 12 for the latest, whereas at Beaverlodge, Alberta, at $55^{\circ} 2' N.$, the same plants started to flower on July 13 and July 21 respectively. The reduction in spread of flowering between the early and late races at stations at intermediate latitudes was progressive from south to north. Moreover, only the earliest varieties thrived and flowered at the most southern stations, whereas all prospered at the more northern latitudes. These results were interpreted as being due to the differential effects of varying temperatures and day lengths at different latitudes on the heading, blooming, and maturing of early and late varieties.

Hugo Glück (1905–1924) studied in great detail many aquatic, amphibian, and marsh plants, both in their native habitats and in cultures at Heidelberg. His extensive morphological and physiological researches upon them are presented in a series of monographs, which contain a wealth of material on the capacities for modification of very many aquatic plants under different environmental conditions.

The effect of factors of the environment upon the morphology of mosses has been studied in detail by Davy de Virvielle (1927). He grew cultures of various polymorphous species and by varying one factor at a time was able to study the effect of differences in light intensity, temperature, and humidity upon their characters, especially those of taxonomic importance. He found that some species reacted more than others to differences in a given variable, and that variation in light intensity and humidity was especially prone to induce morphological changes. Differences in structure were also

marked when species were grown both in aquatic and in terrestrial habitats.

Hans Buch (1928, 1929, 1936), working experimentally with mosses and liverworts in connection with his taxonomic studies, has described modifications which previously were mistaken for distinct species. These were induced by changing certain environmental factors such as nutrition, light intensity, and humidity.

From these examples in the literature it is evident that there is a great amount of evidence that plants can modify their form to a certain extent when exposed to different environments, and that the modifications may sometimes be striking. The range of modification, however, is always governed by the hereditary constitution of the plant. Some species are very limited in their capacity for modification, while others, as pointed out by Massart and others, may undergo appreciable changes.

Various authors have advocated the use of special terms to designate modifications. Linnaeus used *variety*, a term which is now usually applied to groups of distinct heredity. Other proposals include: *accomodat* (Massart, 1902); *ecad* (Clements, 1908); *ecophene* (Tur-esson, 1922*b*); *modification* (Buch, 1928–1936); *epharmone* (Cockayne and Allan, 1927); and *phase* (Cockerell, 1934). Lack of universal acceptance of any of these terms may be due to the different shades of meaning attached to them, but the more likely reason is that there seems to be no real need to designate environmental modifications. Such attempts inevitably lead to difficulty, for the kinds of modification possible are almost as endless as the combinations of external variables that induce them. In the higher groups of plants, at least, existing descriptive methods are ordinarily sufficient to differentiate groups of real taxonomic importance, once they have been determined.

XII

CONCLUSIONS

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The experimental studies described in this volume have dealt with a large number of plants from many unlike species and families. These plants have come from a wide range of habitats. The detailed observations on their behavior in very different environments, covering a number of years, have reimpressed certain facts that seem to be of fundamental importance.

GENERAL PRINCIPLES

There are certain principles that apply generally to all the plant groups studied. These are listed herewith:

1. The individual plant is subject to the interplay between heredity and environment. When grown under different environments it may be quantitatively changed in various degrees. The changes induced by a new environment give no evidence of permanence, but have been shown to be reversible modifications. Some of these changes in vegetative characters are quite spectacular, yet they never obscure the individuality of the plant, which is retained irrespective of the conditions of altitude, light, and moisture in which the plant is grown.

2. Each individual has as part of its inheritance a certain capacity for modification when grown under different conditions. The modifications vary with different species, different races, and even different individuals from the same local population.

3. Modifications are quickly induced. Meristems developing under the changed environment seem immediately to give rise to organs with the modified characters. No evidence suggests yearly cumulative effects on perennial transplants.

4. Variation, of course, is of two sorts: that which is controlled by the environment (modifications), and that which is governed by

the heredity (genetic differences). Both contribute to the differences seen, not only between species and races, but also between individuals of one population. It is essential in following such investigations to keep clearly in mind the distinctions between these two sorts of variation.

5. Each species is composed of an assemblage of races, some of higher order and regional, others more local, graduating down to the individual population and its local variants. The races, regional or local, require many experimental data for their delimitation and elucidation.

6. Species with the widest distribution are observed to have the most races. Conversely, species of narrow distribution have fewer races and are less variable. For example, species exclusively of the lowlands or of high elevations have few distinct races, while those found in both situations have many. Wide latitudinal distribution, or occurrence at both coastal and interior situations, has the same effect, as shown both by Turesson (1930*a*) and by ourselves. Greater differentiation into regional races may therefore be expected in areas with more varied topography and climate, as, for example, in the Pacific Coast states.

7. The regional races of a species are heritably distinct ecotypes, not modifications. Detailed studies, involving records of hundreds of individual plants and their clone members grown simultaneously at different altitudes, show conclusively that there is no tendency for lowland and alpine plants to become morphologically identical when transplanted to the same garden, whether this be situated near sea level, at mid-altitudes, or at timber line. The dwarfing of lowland plants at high altitudes sometimes causes them superficially to simulate alpine, but their essential structural differences are retained. Moreover, physiological differences, as expressed in earliness of flowering and in capacity for survival in specific environments, are often accentuated in such experiments. These conclusions are based on experiments lasting from four to ten and even sixteen years.

8. The regional ecologic units of a complex are in some cases ecotypes, and in others ecospecies. The two sorts of units—ecotypes and ecospecies—are ecologically equivalent, but there is an important evolutionary difference between them.

9. The morphological and physiological differences between ecotypes of one ecospecies may far exceed those between neighboring

ecotypes of two related ecospecies (see *Achillea*, fig. 122, as an example).

10. Each ecotype or ecospecies has a certain range of tolerance for varying environments. This follows from the capacity of their component individuals to adjust themselves to a range of conditions. The degree of tolerance for different environments is a characteristic of the ecotype.

11. The number of ecotypes or monotypic ecospecies into which any cenospecies of a geographic province is differentiated is relatively limited. This follows from the fact that each has its latitude of tolerance. In a transect across central California no more than six or seven regional ecologic units are required in any one cenospecies.

MODIFICATIONS

This volume is replete with examples of modification. Each figure that shows members of a clone as they appear growing at Stanford, Mather, and Timberline illustrates it. We have spoken of the Stanford modification of a plant, for example, meaning the total impression of the Stanford environment on that individual, for modifications affect not only various structural characters but physiological processes as well.

One may interpret modifications from the viewpoint of Klebs (1909), and consider form to be a function of physiology, and the appearance of a plant to be the result of the interaction of environment upon physiological processes—subject, of course, to the limits set by heredity. Essentially the same idea has been expressed by various authors. These include Kerner (cf. p. 395), Raunkiaer (1895–1899, p. xv), and Johannsen (1911). On the basis of the early results of the present investigations, Hall (1932) also discussed the interrelation between heredity and environment.

It is well known that changed temperature, moisture, and light relations will modify the velocity of physiologic processes. It is therefore quite natural that modifications in morphological characters and in manner of development take place in response to transplanting to different environments. Although such modifications may be linked with the tolerance of plants to changed environments, the evidence indicates that ecotypes as a rule are unable to succeed in conditions very unlike those of their native environs.

Physiological characteristics subject to modification include the time of inception of growth following winter dormancy, the rate and duration of growth, the ability to flower, the time of flowering, and the ripening of seed. Numerous examples have been cited of modifications in seasonal rhythm, including the observation that plants at Stanford begin spring growth two to three months ahead of propagules of the same individuals at Mather, which, in turn, are equally advanced over those at Timberline. Instances may be recalled of plants from the vicinity of the coast which are continually active at Stanford, but which have a definite period of dormancy at Mather. The opposite instance is just as interesting, with the alpine forms of *Horkelia fusca* dormant in their native habitat, but assuming the evergreen habit at Stanford. Another spectacular modification in growth habit is the change of the semi-shrubby coastal *Zauschnerias* to perennial herbs at the mid-Sierran station.

The distinction between modifications and hereditary differences was clearly stated by Baur (1914, p. 10), and Turesson (1922*b*) emphasized the fact that modifications may closely resemble heritable variations. That modifications and heritable variations have been confused by many botanists is evident in the literature. There has been a paucity of evidence showing to what extent plants may be modified in different kinds of environment, and how modifications compare with heritable variations. These comparisons have been emphasized in the preceding chapters, for such a study is fundamental to an understanding of plant interrelationships, and of plants in relation to their environment.

THE PRINCIPLE OF REGIONAL DIFFERENTIATION

In all species complexes that cover climatically different areas, the phenomenon of regional differentiation stands as a fundamental principle. Its operation has already been shown by Turesson in many European species of plants. Our results from west American groups not only substantiate Turesson's general conclusions, but also add many facts. These have come to light largely because the transplants were studied at three altitudes instead of at one only, and because the environments in California are very different from those of northern and middle Europe.

The latitude of the California transect is that of the southern

Mediterranean. There is also considerable geomorphological difference between California and middle Europe. The California mountains follow a north-south direction transverse to the prevailing winds. They parallel the coast, rarely leaving room for an extensive coastal plain. The mountains of middle Europe follow an east-west direction and are distant from the sea. Therefore, as compared with the region from which Turesson's plants came, the California region has more climatic belts which change rapidly and abruptly as one moves inland from the ocean.

THE DISTRIBUTION OF ECOTYPES AND ECOSPECIES. Regional differentiation may be expressed either as a series of ecotypes belonging to one species, or as a series of closely related ecospecies, or, more commonly, by both. Whatever the means of differentiation, the ecological result is the same, namely, that each climatic region is occupied by forms particularly suited to that environment. In *Potentilla glandulosa*, and probably in *Sisyrinchium bellum*, one species has been able to occupy almost the entire transect across central California by a simple differentiation into ecotypes; in the *Achillea millefolium* complex the same transect has been covered by two ecospecies, and in the *Artemisia vulgaris* complex by three, some of which are differentiated into ecotypes.

Ecotypes and ecospecies of one complex frequently cover this area rather continuously, substituting one for another. The belts they occupy fluctuate in conformity with topographic irregularities and resultant climatic changes. This complicates their distribution and causes a moderate amount of overlapping. Where ecotypes or ecospecies of one complex meet, they may occupy locally different habitats, as in *Potentilla glandulosa*, where the foothill ecotype, ssp. *reflexa*, occupies the drier slopes, while the meadow and subalpine ecotypes, sspp. *Hanseni* and *nevadensis*, tend to occupy the moister meadows. Hybrids are found at such localities.

DIFFERENCES IN DISTRIBUTION OF SPECIES. There are great differences in the capacity of species and complexes to occupy this area. This is shown in figure 154, which illustrates the distribution of the Potentilleae along the transplant transect in central California.

Potentilla glandulosa occurs in the Coast Ranges from near sea level upward, but avoids the lowest altitudes of the interior valleys. It reappears in the Sierra Nevada at 225 m. and is a characteristic

occupant of moist draws, open meadows, and slopes up to over 3350 m. On the eastern slopes of the Sierra Nevada it grows only at high altitudes and does not occupy the Great Basin except in the mountains.

Potentilla gracilis, on the other hand, is not found in the central Coast Ranges, but covers the Sierras from about 1000 m. to alpine altitudes on the west slope and occurs even in the Great Basin. A related ecospecies, *P. diversifolia*, is restricted to alpine conditions, and another, *P. pectinisecta*, occupies only the dry Great Basin. A characteristic difference between the members of the *glandulosa*

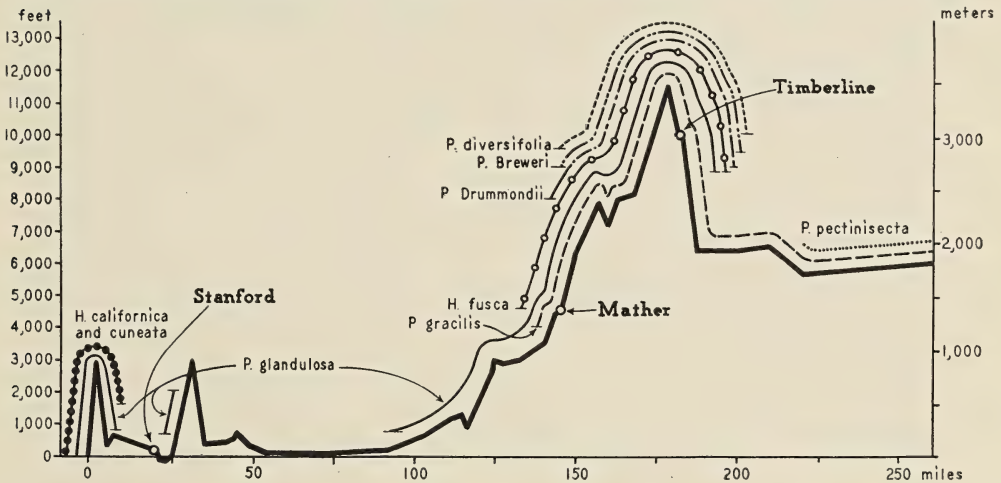


FIG. 154. Altitudinal distribution of certain Potentilleae in the California transplant station transect. (See fig. 1 for orientation.)

and the *gracilis* complexes in California is that the latter do not approach the coast, but are able to populate desert flats east of the Sierra, while those of *glandulosa* flourish only on the west-facing slopes.

The *Potentilla Drummondii* complex is an example of a group restricted to subalpine and alpine altitudes. One of its species, *P. Breweri*, is strictly alpine. In the genus *Horkelia*, a Sierran species, *fusca*, occurs from mid-altitude to alpine conditions, whereas other species, like *H. californica* and *cuneata*, are found only in the coastal region. Similar differences in the capacity of species to occupy various climatic belts of California were discussed in chapter VI for *Zauschneria*, and for other groups in other chapters.

The Lower Sonoran zone, in which the Great Valley of California

is located, is usually not occupied by the perennials that entered into the transplant experiments. It is too dry and hot for this mainly northern floral element. Annual members of the Madiinae, a subtribe of the Compositae extensively studied by us, occupy these valleys and the Sierran foothills, the Coast Ranges, and the maritime zone, but they have been unable to occupy the higher elevations. We know of no one species that has developed races for both the alpine and the Lower Sonoran zones.

PARALLEL DIFFERENTIATION IN NON-ADJACENT AREAS. Can a species develop parallel ecotypes in different parts of its range, where corresponding ecologic opportunities are offered? Several examples suggest an answer.

The alpine *Potentilla glandulosa nevadensis* is mainly restricted to California and Oregon, but in the alpine regions from Washington to Montana it is replaced by ssp. *pseudorupestris* and in southern Utah and Arizona by ssp. *arizonica*. Only *pseudorupestris* appears to be directly related to *nevadensis*. In the southern Rocky Mountains the rôle of the alpine ecotype has been taken over by another species of the same complex, *P. fissa*, although forms of *P. glandulosa* occur near by at lower elevations.

Potentilla gracilis has an alpine ecotype in the Sierras, but farther east it extends only to subalpine elevations; the alpine altitudes in the Rocky Mountains are occupied by its close relative, *P. pulcherrima*. *Artemisia ludoviciana* and *Achillea lanulosa*, however, have similar alpine forms in both the Sierras and the Rockies.

A complete analysis of a number of ecotypes in addition to those from California would be necessary before any suggestions could be offered as to causes for differences in distribution of west American alpiners.

Turesson (1925, 1931b) pointed out that some species that cover the mountainous regions in both Scandinavia and central Europe have developed alpine ecotypes in only one of these areas, whereas other species have alpine ecotypes in both. *Melandrium rubrum* and *Solidago Virgaurea* have alpiners only in Scandinavia, *Silene venosa* and *Trifolium pratense* only in the Alps, although all four are common in both areas.

MINOR DIFFERENTIATIONS WITHIN ECOTYPES. Each of the regional ecotypes contains a complex of biotypes. Not only is there consid-

erable variation within the population, but race complexes are also in evidence, as for example in the series of *Potentilla glandulosa* ssp. *reflexa* from Tuolumne Canyon. The plants of this foothill ecotype climb to rather high elevations on warm slopes of this canyon. Those that occur at the higher habitats have the lower stature in a uniform garden, but they show no difference in earliness.

Likewise, there are places where ecotypes are evidently in the process of development, such as the apparently rudimentary maritime ecotype of *Potentilla glandulosa* (fig. 14), and the partially differentiated alpine ecotype of *Potentilla gracilis*, growing with plants of subalpine character in populations around Timberline station.

The picture is further complicated by evidence of hybridization where ecotypes meet. The effects of hybridization diminish often at some distance from the point of contact, although genes probably may migrate for long distances.

Another cause for complexity within the ecotypes is that several characters may recombine, including those of importance for survival. An example is earliness and frost resistance in an alpine *Potentilla gracilis*. Some are able to seed themselves in the alpine environment because of their earliness, others because of their frost resistance. Although plants possessing both properties may be the best fitted for the environment, a mixture of biotypes showing recombinations of these characteristics is found in populations surrounding Timberline station.

Accordingly, the individual ecotype itself presents a complex picture. It may, however, be statistically distinguishable from other ecotypes in characters of importance for survival in a given habitat. Such complexity is to be expected in a dynamic world.

CHARACTERIZATION OF CALIFORNIA ECOTYPES AND ECOSPECIES. From the transplant results some general characteristics of the ecologic units in various climatic regions of California are observed. These are summarized below. In this characterization no distinction is made between ecotypes and ecospecies.

MARITIME AND COAST RANGE FORMS

The forms from the Coast Ranges and from the immediate coast have much in common. The latter are the more extreme and occur on the west side of the outer Coast Ranges, or are limited to a narrow strip exposed directly to the ocean.

1. The maritime and Coast Range ecotypes (or ecospecies) are in more or less active growth throughout the year at the lowland station. If they have a rest period, this is usually in the late summer, and new growth begins with the advent of winter rains.

2. They flower early at Stanford, but are delayed at the mountain stations.

3. Frequently their herbage is relatively frost-resistant, a characteristic which enables them to grow during the cool rainy winters.

4. When transplanted to Mather, they usually become reduced in size. Coast Range ecotypes tend to survive indefinitely there, whereas maritime ecotypes and ecospecies as a rule succumb within a few years.

5. They are unable to set ripe seed at Timberline, and rapidly decline there and die, although the hardier species may survive a winter or two.

The perennials discussed in preceding chapters usually have coastal ecospecies rather than maritime ecotypes. An exception is *Sisyrinchium bellum*. The coastal ecospecies have been less extreme in their morphology and less restricted in their distribution than the truly maritime ecotypes observed in the annual Madiinae. The latter are prostrate or short-stemmed and limited to bluffs and slopes directly facing the ocean.

FOOTHILL AND MID-ALTITUDE FORMS

Most species have one or the other of these ecotypes, but some, such as *Potentilla glandulosa*, have both.

1. The foothill forms have a short period of dormancy at Stanford during the winter months, and a long rest period at Mather.

2. The mid-altitude ecotypes flower later at Stanford than the Coast Range ecotypes, but they are earlier at Mather.

3. Their herbage is not frost-resistant, so these ecotypes become dormant when frosts begin.

4. Usually they reach their maximum growth and are tallest at Mather; if they survive at the alpine station, they are much reduced.

5. At Stanford they may survive well, but some are attacked by disease. At Timberline they flower too late to produce ripe seed, or fail to reach the flowering stage (*Zauschneria*), or even fail to survive.

SUBALPINE AND ALPINE FORMS

These ecotypes differ from each other in size and earliness, the alpiners being the dwarfer and the earlier.

1. Both have a definite period of dormancy even at the lowland station—longer than that of mid-altitude forms. An exception is *Horkelia fusca*, which becomes evergreen at Stanford.

2. Subalpiners are usually a little earlier than mid-altitude forms at all stations, while alpiners are considerably earlier. In some groups, the alpine and subalpine ecotypes are unexpectedly delayed in flowering at Stanford, but not at Mather.

3. Alpiners are often more frost-resistant than subalpiners, and usually consid-

erably more so than mid-altitude forms. There is often great individual variation in this respect.

4. All subalpines and most alpines increase in height and vigor at the mid-altitude station. At Stanford their vigor and stature are lessened, as a rule.

5. Both the subalpine and alpine ecotypes survive at Timberline, but only the latter matures seed there every year. Races of some species that are native around the alpine station mature only in exceptionally long seasons and are considered to be subalpines that are pioneering in an alpine environment. At Stanford both ecotypes may survive, but many alpines are short-lived and not very floriferous, and may even remain vegetative for years. Some are attacked by diseases, and many emerge from their winter dormancy in a visibly weakened state, but regain strength during the summer.

GREAT BASIN FORMS

Data from Great Basin forms are not as complete as from the others. In general, they react much like mid-altitude plants. They are, however, more frost-resistant, and usually survive better at Timberline, even though they are unable to mature seed there. Most of them thrive at Mather, but *Potentilla pectinisecta* is an exception in being notably weak at this station. At Stanford Great Basin forms grow and survive fairly well.

PLANTS FROM HIGH LATITUDES

Plants of certain species from high latitudes in northern Europe were found to grow well at Stanford, including *Achillea millefolium*, *Artemisia vulgaris*, *Viola canina*, and *V. Riviniana*. Others show a marked decrease in size and vigor, as, for instance, *Potentilla rupestris*, *Epilobium angustifolium*, *Carex macloviana*, and *Deschampsia caespitosa*; also *Achillea borealis* from Alaska.

THE BASIS FOR REGIONAL DIFFERENTIATION

Regional differentiation of the species complex to fit various climatic zones appears to be general. The transplant experiments have shown that the regional races are not environmental modifications, but are heritably different. Whenever the ecotypes have been tested by breeding, as in *Zauschneria*, *Potentilla*, and in many unpublished cases of *Madiinae*, they have proved to be constant in that they reproduce their kind. What is the basis for the differences between ecotypes? Are genic or chromosomal differences involved, or both? Of the perennial plant groups investigated, most have both genic and chromosomal differentiation, but in some cases species with a constant number of chromosomes occupy very different environments. Changes in the number of chromosomes are, of course, basically

genic, for the complex balance among all genes in all the chromosomes is altered. This viewpoint has been crystallized through the results from the investigations on *Datura* (Blakeslee, 1931).

DIFFERENTIATION WITHOUT DIFFERENCES IN CHROMOSOME NUMBER. *Potentilla glandulosa* is an outstanding example of genic differentiation alone. The genetic differences between its alpine and foothill ecotypes have been discussed (see pp. 116–124). It was determined that both morphological and physiological characters showed genetic segregation, and that such characters evidently depend upon a series of genes with minor effect. The existence of genetic linkage between taxonomic characters and those of importance for survival of the ecotypes was also pointed out. Similar complex segregations were observed in hybrids between ecotypes of *Zauschneria*. These and unpublished experiments on hybrids between ecotypes of *Madiinae* indicate that differentiation is produced by numerous genes of the multiple type, each with a cumulative effect. Mutations and hybridization may have worked hand in hand to produce regional differentiation. Furthermore, absorption of genes from related eco-species may contribute to the variation.

DIFFERENTIATION WITH DIFFERENCES IN CHROMOSOME NUMBER. When the chromosome number changes, free intercrossing between the groups is prevented, and a species difference has been set up. Within a cenospecies, differences in chromosome number ordinarily mark the limits of ecospecies. Such differentiation may sooner or later become accompanied by genic differentiation.

A summary of the results of both kinds of differentiation from the more important groups in central California that we have investigated is shown in figure 155. This diagram is intended to represent the approximate distribution of each species complex along the transplant station transect, the extent of its ecotypes or ecospecies, and the chromosome numbers. Three cases of simple genic differentiation without change in chromosome number are represented.

The first complex that is represented by only one chromosome number is *Sisyrinchium bellum*. It probably constitutes a single species that has differentiated ecotypes for maritime, Coast Range, mid-altitude, alpine, and Great Basin environments. It is still an open question whether a distinct subalpine ecotype can be recog-

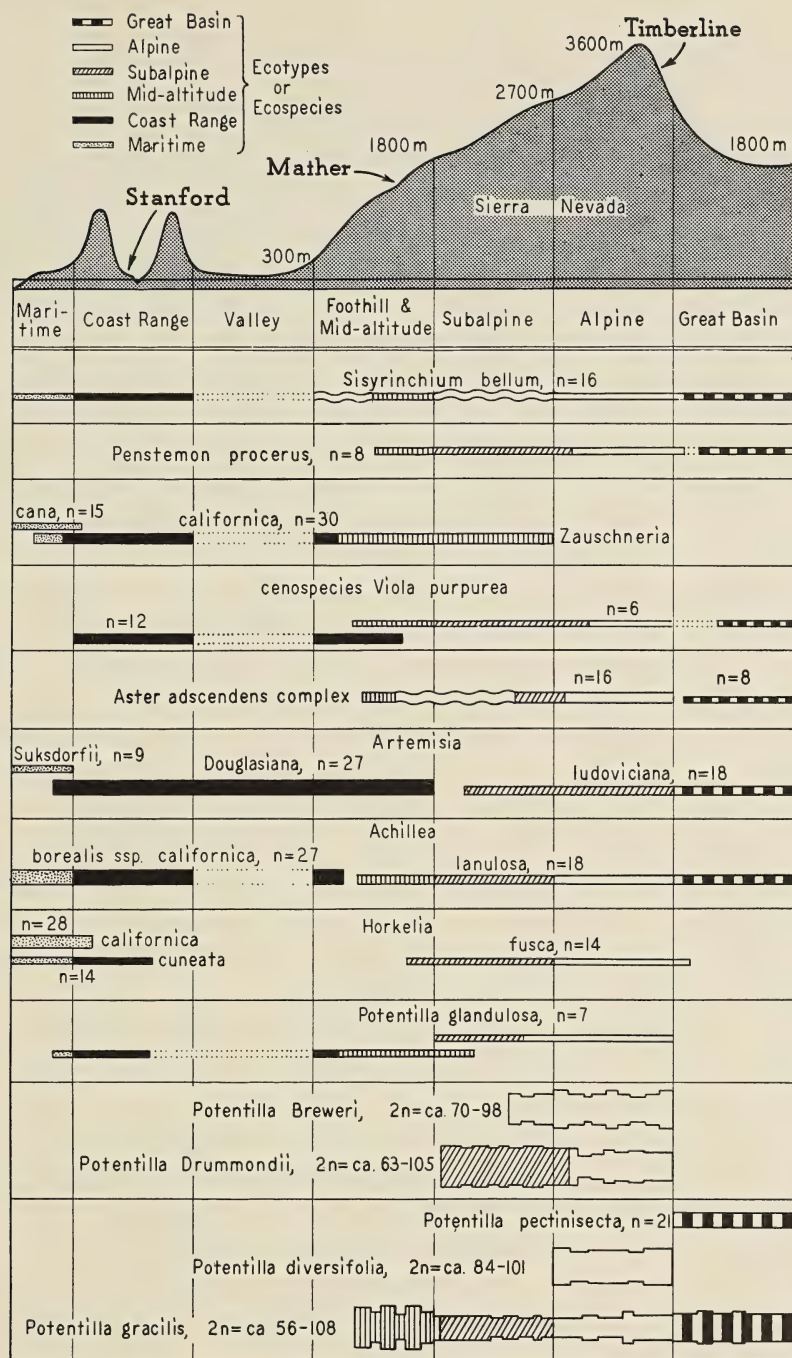


FIG. 155. Distribution of ecotypes and ecospecies in a transect across central California.

Dotted lines indicate absence of forms; wavy lines, exact boundaries of ecotypes not established. Width of symbols indicates chromosome number and is roughly proportional to the degree of polyploidy. Names refer to ecospecies. The alpine ecotypes occur only up to about 3100 to 3300 m. altitude.

nized in this species, hence the wavy line in that zone. Some of the ecotypes of *Sisyrinchium* are shown in figure 141.

The second example is *Penstemon procerus*. This species does not occur in the Coast Ranges, but mid-Sierran, subalpine, alpine, and Great Basin ecotypes are found. Some of these are shown in figure 107.

Potentilla glandulosa furnishes the third example, and has produced ecotypes for all the major climates in the region except the Great Valley and the Great Basin, although its maritime ecotype is no more than incipient. The overlapping of foothill and subalpine ecotypes is indicated, but the more limited meadow ecotype, which occurs in this zone of overlapping, is omitted. Illustrations of its ecotypes are found in chapter II.

The other cases indicated in the graph represent species complexes in which the chromosome number changes somewhere along the transect. Differentiation in these involves both ecospecies and ecotypes. The examples studied happen to be all of the polyploid type, none being "aneuploid" or dysploid (a term coined by Tischler, 1937a).

Zauschneria is a cenospecies with a diploid ecospecies, *Z. cana*, in the coastal region, and a tetraploid species, *Z. californica*, from the coast to subalpine altitudes. The diploid species is monotypic, but the tetraploid is differentiated into a maritime ecotype, ssp. *angustifolia*, a Coast Range ecotype, ssp. *typica*, and a mid-altitude ecotype, ssp. *latifolia*. The last-named form extends upward to 2700 m., but it is rare above 1800 m. and all its members in the experiments react the same way as mid-altitude plants. These units are shown in figures 84 and 85.

The cenospecies *Viola purpurea* was not mentioned in the previous text, but it is the subject of papers in preparation by M. S. Baker and J. Clausen. It contains two ecospecies, a tetraploid in the Coast Ranges and Sierran foothills and a diploid in the Sierras and the Great Basin. The latter has developed morphologically distinguishable mid-altitude, subalpine, alpine, and Great Basin forms; therefore, in this cenospecies the greatest variation and ecologic adaptability are shown by the diploid species, not by the tetraploid as in *Zauschneria*.

In the *Aster adscendens* complex there are at least two members in a polyploid series. In this case it is the Sierran species that is tetraploid, whereas the supposedly primitive diploid species is found

in the climatically extreme Great Basin. The tetraploid includes mid-altitude, subalpine, and alpine ecotypes (see fig. 149).

In *Artemisia* there is again a new pattern. The diploid *Suksdorfii* is strictly maritime. The tetraploid member of the complex, *A. ludoviciana*, is a species of the Great Basin and the Great Plains, but it has developed a high-montane ecotype. This ecotype is subalpine in transplant reaction, not alpine. The hexaploid *Douglasiana* occupies the zones between the diploid and the tetraploid species from the coast to mid-altitudes in the Sierras, including even the Great Valley. It appears to consist of only one ecotype, although it occupies climatically different zones. Figures 128 and 129 show examples of the *Artemisia* complex.

The Achilleas of the *millefolium* complex are differentiated into a tetraploid and a hexaploid ecospecies with no diploids known. The hexaploid *A. borealis* occurs from the coast to the Sierran foothills, being absent in the Great Valley. It has a distinctly maritime and a Coast Range ecotype. The tetraploid *A. lanulosa* has developed the usual three Sierran ecotypes in addition to the one in the Great Basin (see figs. 117, 122).

Horkelia californica (fig. 83), which is tetraploid, and *H. cuneata*, which is diploid, are maritime species. The diploid has been able to produce a Coast Range ecotype, while the tetraploid has not. Neither of these occurs in the Sierras, but the diploid *H. fusca* (fig. 78) is found at higher elevations there, and covers an appreciable altitudinal range, although it appears to be composed of only subalpine and alpine ecotypes. The basic chromosome number in this genus is 14, as compared with 7 in *Potentilla*.

The *Potentillas* of cenospecies *Drummondii* and *gracilis* present a picture of chromosomal irregularity with high polyploidy, which is presumably associated with facultative apomixis. They vary in chromosome number within the ecotype and even within the population. Most remarkable is the fact that the ecotypes are fairly well differentiated in spite of the oscillating chromosome number.

In cenospecies *Potentilla Drummondii* the deca- to 14-ploid *P. Breweri* has evolved only an alpine ecotype (see fig. 72). *Potentilla Drummondii*, however, developed both subalpine and alpine ecotypes (fig. 71). There is probably no significant difference between the chromosome numbers in the subalpine and the alpine ecotypes.

In the cenospecies *Potentilla gracilis* the only member that is cy-

tologically regular is *Potentilla pectinisecta* (see fig. 53, lower), a hexaploid species of the arid Great Basin. Members of this ceno-species with high and oscillating numbers are found in the more mesophytic climates of the Sierra Nevada and other ranges.

Potentilla diversifolia (see fig. 55), another member of the *gracilis* complex, has evolved only an alpine ecotype, whose chromosome number varies from 12- to 14-ploid. *Potentilla gracilis* (fig. 49) has the greatest variation in chromosome number of any member of its complex; it has also the widest altitudinal and geographical distribution. Four major ecotypes are found, ranging from the nona- to 16-ploid mid-altitude ecotype, through the octo- to 12-ploid subalpine and alpine ecotypes on the west side of the Sierras, to the Great Basin ecotype, in which 12-ploid forms have been found. In this species there is some tendency for plants with the highest chromosome numbers to be found at lower elevations. All the four ecotypes of *P. gracilis* belong in one morphological subspecies.

The examples summarized in figure 155 present an illuminating picture of the variation found in nature. No two plant groups in this list, which covers the main subjects of these experiments, have identical patterns of distribution. Scarcely two are closely similar. Yet, the major ecotypical differences are found over and over again in slightly different patterns.

Turesson (1925) found four regional hereditary adjustments in plants of central and northern Europe. These were the maritime, lowland, subalpine, and alpine ecotypes. The chromosome numbers of most of these have not yet been systematically determined, although, according to a recent paper (Turesson, 1938), twenty-five of the species appear cytologically constant over large areas. In addition to these a few polyploid complexes similar to the Californian were found. Such complexes were *Galeobdolon luteum* with a tetraploid race ($n=18$) in Bavaria and a diploid ($n=9$) farther north in Sweden and Latvia, and *Sedum telephium*, which is diploid ($n=12$) in the vicinity of Vienna, Budapest, and Moscow, and tetraploid ($n=24$) in Sweden and Siberia. From these data it is therefore impossible to determine accurately to what extent polyploidy has been a factor in ecological differentiation in northern and middle Europe.

HAS CHROMOSOME NUMBER AN ECOLOGICAL SIGNIFICANCE? It is obvious from this survey along the transplant transect that closely

related plants differing in chromosome number usually occupy different environmental niches. The groups do not agree as to where the cytologically primitive forms with the lowest chromosome numbers are located. In some instances they are along the sea, in others in the high mountains, and in still others in the desert. From this the conclusion is reached that the hereditary differences observed so generally in plants along the transect are not correlated with differences in the number of their chromosomes, but strictly with the environment.

This view becomes still more evident as we study the literature bearing on this subject. Until very recently an opinion has been rather widespread that in polyploid complexes, forms with the higher chromosome numbers occupy the more adverse environments. Recent literature, however, is replete with examples that substantiate the observations made in the present investigations that there is no support for this view.

The correlation between differences in chromosome number of closely related species and their ecology was first brought to attention by Hagerup (1927, 1928, 1932) in his investigations on *Empetrum*, on the Ericaceae of arctic and middle European distribution, and on other plants from the southern part of the Sahara. From this study he concluded that polyploids are associated with extreme or unfavorable environments. However, after discovering that in the *Vaccinium uliginosum* complex the diploid form *microphylla* is strictly arctic, while the tetraploid *genuina* is arctic and northern temperate, Hagerup (1933) altered the formulation of his theorem to read: "Polyploid forms may be ecologically changed so as to grow in other climates and formations where the diploid form will not thrive." There is nothing in our findings to conflict with this statement.

Shimotomai (1933), Tischler (1936, 1937*a*, 1937*b*), and Rohweder (1936, 1937) have emphasized that maritime plants tend to have high chromosome numbers. That this is no general rule is shown by the present investigations, where the coastal species are diploid in three complexes and tetraploid in only one. The investigations on chromosome number and distribution by the Tischler school are based on statistics in which a chromosome number is assigned to each species as a whole, not on counts of races from distinct habitats.

The risk one assumes in determining the chromosome number of a species by counting only those of one race is clearly shown in the investigations by Manton (1934, 1937) on *Biscutella laevigata*. This proved to be a complex that has a diploid species in the nonglaciaded lowlands of middle Europe and a tetraploid species in the Alps. Griesinger (1937) found similar cytological differences in *Arenaria serpyllifolia*, but here the distribution was reversed: the alpine subspecies was diploid, while the lowland and subalpine forms were tetraploid. Fagerlind (1937, p. 354) discovered that *Galium verum* and *G. Mollugo* similarly are

polyploid complexes. Here the diploids are southern, and center in the Balkans, while the tetraploids are found in middle Europe, Scandinavia, and England. But in the *Campanula rotundifolia* complex (Böcher, 1936), the more southern forms from Denmark are tetraploid, while the arctic forms from Greenland are diploid and tetraploid, as in *Vaccinium uliginosum*. An example of chromosome difference between the American and the European components of a circumpolar complex is *Potentilla fruticosa*, which is diploid ($n=7$) in Alberta, Canada, and tetraploid ($n=14$) in islands of the Baltic, near the type locality (Turesson, 1938).

Another example of correlation between chromosome number and distribution is the *Iris versicolor* complex of the eastern United States (Anderson, 1936). *Iris setosa* is the most northern and has the lowest number of chromosomes ($n=19$), *I. virginica* ($n=35$) is the most southern, and the allopolyploid *I. versicolor* ($n=54$) is found between its supposed parents. Another pattern of distribution was observed in *Tradescantia* (Anderson and Sax, 1936), with the diploid and the tetraploid forms cohabitant. No morphological differentiation had taken place between diploids and tetraploids in this genus.

The extensive literature on the subject of polyploidy has recently been discussed by Müntzing (1936). Further examples have been mentioned there. In evaluating his conclusions it must be remembered that Müntzing's definition of autopolyploids (p. 311) would include many allopolyploids whose parents belong to different species.

Generalizations based on few examples should be considered critically. Suggested correlations between chromosome numbers and size, environment, earliness, and other characteristics of plants have proved to be specific, not general. Examples of contradictions to commonly accepted trends include the octoploid *Artemisia Rothrockii* of the high mountains, which is earlier than its close diploid relative, *A. Bolanderi* of the desert flats. Likewise, *Potentilla diversifolia* is distinctly earlier and more dwarfish than the closely related alpine *P. gracilis*, although its chromosome number is higher. On the other hand, the diploid *Artemisia Suksdorffii* is earlier than its tetraploid and hexaploid close relatives, but it is of maximum size.

If we relate these results to the actions of the genes in the chromosomes rather than to an effect of the chromosome number itself, then it is quite understandable that polyploidy does not have the same effect in all plants. With many genes in action, some delaying and others accelerating the processes, and some decreasing, others increasing the size of plants, it is to be expected that autopolyploidy will produce different effects, depending upon the kind of genes in preponderance in the original stock.

Balances of this nature probably determine the fate of the poly-

ploids. Doubling of all genes in an autopolyploid would be expected to shift the physiology of the plant, because the balances are so delicate. If this happens, the plant may be able to occupy a new environment. Differential selection then may effect secondary changes in morphological appearance, so that the polyploid may become a distinguishable taxonomic species. This differentiating factor is not operative if the diploid and the polyploid remain in the same environment, and a situation results like that in *Tradescantia*.

An allopolyploid similarly depends upon the balances in the genomes of its parental species. Because of the many genes involved, we should expect an allopolyploid ordinarily to be intermediate, both in appearance and in physiological makeup. We usually find it lodged between its probable parents in nature. It may even crowd out one of its parents or another member of the cenospecies.

The discovery of a high percentage of polyploids in perennials from the Sierran transect has aided in solving some of the difficult taxonomic problems. It also impresses us with the probable importance of polyploidy in plant evolution in certain environments. When Winge (1917) published his theory on the origin and importance of chromosome numbers, it was impossible to foresee how fruitful the study of polyploidy would become within the next twenty years. We do not yet know whether polyploidy is equally frequent in all environments. Investigations on plants from other parts of the world in different environments with different geologic histories are needed before this question can be answered.

EQUILIBRIUM BETWEEN PLANT AND ENVIRONMENT

Natural selection doubtless determines the character of the plants that occupy a given environment. Since physiological processes, which change in rate with differences in temperature, moisture supply, and other external variables, are profoundly influenced by environment, successful plants must be fairly accurately adjusted to their surroundings. When they are removed from this environment and brought to a climatically different region, their physiological processes will act at a pace determined by the physical conditions of the new environment, and by heredity. If the plant's heredity is such as to enable it to accommodate itself to the new environs and to compete, the plant may prove to be a success in the new climate.

It may be more or less successful than it was in its original home, depending upon the accuracy of its adjustment to the new surroundings. The chances are, however, it will be less successful, because its very existence in its original habitat bears testimony to its superior suitability for that kind of situation as compared with plants that are not found there.

In the earlier chapters, many examples of disturbances in equilibrium between transplanted individuals and their new environments were described. Among the most conspicuous examples were lowland plants that were unable to complete their annual cycle in the alpine environment, and alpine plants that grew with much reduced vigor and flowering in the lowland environment. Furthermore, certain plant groups are more specialized in their requirements than others. Some alpine plants, for example, are distinctly unsuccessful when brought to the mid-altitude station at Mather, while others become even more vigorous than in their native alpine environment. In the latter instance we infer that it is not the physiological unsuitability in itself that keeps them from occupying the mid-altitude environment, but some other factor, such as competition from genetically taller races.

The reaction patterns observed after transplanting various groups of plants indicate that the interrelation between plants and their environment is very complex. No two plants are exactly alike in this respect, although they arrange themselves into certain major groups according to their reactions.

RELATION BETWEEN INTERNAL AND EXTERNAL EQUILIBRIA. Not only must a plant be in equilibrium with its environment in order to succeed, but its entire gene activity must be in balance. Even a single pair of genes of the sublethal type may throw the physiologic processes entirely off balance, but individuals with such genes face elimination by selection. Hundreds, possibly thousands of genes interact in each individual, all influencing the plant slightly in one direction or another. Of necessity, all processes regulated by them must be synchronized in the proper order and adjusted to the environmental conditions if the plant is to succeed.

Experiments have shown that the *ecosppecies* is composed of a group of individuals that can exchange genes with each other without disturbing this internal balance. Considering the great morpho-

logical and physiological dissimilarities between alpine and foothill ecotypes of a species like *Potentilla glandulosa*, one wonders that a system so intricate can be so well synchronized.

Each ecospecies represents a different equilibrium. When two species exchange their genes the balance is upset, as for example in the hybrid of *Zauschneria cana* \times *septrionalis* (fig. 102) and scores of *Madiinae* and *Viola* hybrids.

In view of these exacting requirements, it is understandable that evolution is a slow process. It is to be expected that a certain inertia against changes may be experienced in a system of this nature, for it is not a simple matter to develop a new equilibrium to meet the demands of an environment. The very nature of the double demands of internal balance and fitness to the environment is evidently the most important cause of the apparent discontinuity in nature.

APPLICATIONS TO CROP BREEDING. Cultivated plants have to meet essentially the same requirements as plants in the wild. They have their ecotypes or agrotypes just as the wild species have. In general, the more they resemble wild plants in being able to take care of themselves, the more successful they will be. Crop plants have some advantage over those in the wild through the removal of competing plants, and through benefits from cultivation practices. However, these factors merely modify, and do not alter, the operation of the principles outlined above.

The transplant experiments suggest that yield depends to a large extent upon the adjustment between a plant's heredity and its environment. The problem of the breeder is to produce strains to fit a given environment. The unpredictable reactions observed in the transplant experiments indicate the need for test stations located in environments generally similar to those in which the crop is to be grown.

THE NATURAL UNITS

The ecotypes and ecospecies are the natural ecologic-evolutionary units. They are built from many genes into complex morphologic-physiologic-cytogenetic systems. Both ecotypes and ecospecies may differ by many morphological characters, in addition to many of a purely physiological nature. Each character is usually determined not by one but by many genes, each with minor cumulative effects, giving a blended type of segregation. There is no fundamental dif-

ference between ecotypes and ecospecies with respect to their gene differences. These so-called modificatory genes may be the most important in evolution—a conclusion reached by Baur (1924, 1932), Tammes (1925), and East (1935).

Ecotypes are grouped into ecospecies, and ecospecies, in turn, into cenospecies. The cenospecies is made up of the ecotypes of one or more ecospecies. Its ecologic subunits occupy separate niches within the area of the complex. Gene exchange is still possible between these subunits, but not between different cenospecies. This makes the cenospecies a unit of superior evolutionary importance. In most cenospecies evolution is probably still going on. Related cenospecies are only able to add their genes by the rare formation of new species through allopolyploidy.

A species with many ecotypes is for evolutionary purposes a more flexible unit than a series of monotypic ecospecies. The least flexible pattern of differentiation is a series of monotypic cenospecies.

Species building requires many tools. Simple gene changes are among the first of these. They are expressed in gradual morphological differentiation. Natural units are found that represent transitional stages of genetical and morphological separation. Some ecotypes are still imperfectly differentiated, while others are on the way to becoming independent ecospecies. From the presence of all stages of differentiation in nature, we infer that purely genetic separation is a very slow evolutionary process.

In other instances chromosome differences, such as polyploidy, may arise suddenly and permit the species population to migrate into a new environment. In this case morphological differentiation is ordinarily a secondary process aided by isolation and selection in a new environment. In sexual species diploids and polyploids of one complex rarely inhabit the same territory. An allopolyploid is almost predestined to occupy a different habitat from its parents, because they fit ecologically unlike regions.

Dysploidy (“aneuploidy” of usage) is still another pattern of differentiation. This course of evolution has been followed by the Cyperaceae and the greater number of the California Madiinae. A principal difference between polyploidy and dysploidy is that the latter will tolerate single chromosome differences, while in the former the entire diploid genom acts as a superchromosome.

Reorganization within the chromosomes through inversions or re-

ciprocal translocations is still another pattern. The result has often the effect of a premature interspecific differentiation. The gene content remains the same in the new form and its parent, and the ecological requirements are unchanged, but the chromosome rearrangements, if sufficiently numerous, may render the forms entirely intersterile. Secondary changes, altering their ecologic requirements, may aid some of the forms to migrate to new environments, with subsequent morphological differentiation. Outstanding examples of this kind of differentiation are the *Drosophilas* (Dobzhansky, 1937) and the genus *Holocarpa* of the Madiinae.

Evolutionary processes have left plants arranged in groups of various order and separation, such as ecotypes, ecospecies, and ceno-species. These groups indicate stages in the evolutionary differentiation. Ecotypes and ecospecies are features of regional differentiation within the cenospecies, and they have evolved only where there is a diversity of environment.

There are many ways in which living things can increase their variation, but regional differentiation requires the discriminating selection offered by unlike environments. We have no evidence that the direct influences of the environment produce fundamental hereditary changes in species, but major alterations in environments provide new habitats and refuges for the products of nature's continual experimentation among all the plant species that populate a given area.

LIST OF CHROMOSOME NUMBERS FOUND IN PLANTS OF THE PRESENT EXPERIMENTS

GRAMINEAE

	PAGE
<i>Phleum alpinum</i> L., alpine, Sierra Nevada, California, $n=14$. . .	352
<i>Sitanion Hystrix</i> (Nutt.) J. G. Smith, $n=14$	352

CYPERACEAE

<i>Carex festivella</i> Mkze., $n=45$	355
<i>C. macloviana</i> d'Urv., Swedish Lapland, $n=ca.$ 41-43	358

IRIDACEAE

<i>Sisyrinchium bellum</i> S. Wats., maritime, mid-Sierran, alpine, and Great Basin forms, $n=16$	363
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RANUNCULACEAE

<i>Thalictrum Fendleri</i> Engelm., alpine form, $n=14$	365
Mid-Sierran form, $n=28$, and $ca.$ 35	365

ROSACEAE

Potentilla rupestris complex

<i>Potentilla arguta</i> Pursh ssp. <i>typica</i> Keck, $n=7$	30
<i>P. glandulosa</i> Lindl., $n=7$	30
The following subspecies and ecotypes were investigated:	
sspp. <i>typica</i> Keck, <i>reflexa</i> (Greene) Keck, <i>Hanseni</i> (Greene)	
Keck, subalpine and alpine ecotypes of <i>nevadensis</i> (S.	
Wats.) Keck, <i>globosa</i> Keck, and <i>arizonica</i> (Rydb.) Keck.	
<i>P. rupestris</i> L., $n=7$	30

Potentilla gracilis complex

<i>Potentilla gracilis</i> Dougl. ssp. <i>Nuttallii</i> (Lehm.) Keck, $2n=ca.$	
52, 54, 56, 57, 58, 59, 62, 63, 64, 68, 70, 72, 78, 80, 84, 101,	
103, and 109	172-173
Mid-altitude, subalpine, alpine, and Great Basin ecotypes	
investigated.	
<i>P. diversifolia</i> Lehm., $2n=ca.$ 84, 91, and 101	173
<i>P. pectinisecta</i> Rydb., $n=21$	173

- P. flabelliformis* Lehm., $2n=ca.$ 60–65 in five plants 173
P. pulcherrima Lehm., $2n=ca.$ 70, 71, and 108 173–174

Potentilla Drummondii complex

- Potentilla Drummondii* Lehm. ssp. *typica* Keck, $2n=ca.$ 92, 96,
 100, 104, 105, and 108 194
P. Drummondii ssp. *Bruceae* (Rydb.) Keck, $2n=ca.$ 64, 69, 71,
 79, 87, and 98 194
P. Breweri S. Wats., $2n=ca.$ 72, 100, and 102 194–195

VIOLACEAE

- Viola adunca* J. E. Smith sspp. *typica* M. S. Baker, *oxyceras*
 Piper (including *V. retroscabra* Greene), *Ashtonae* M. S.
 Baker, and *radicosa* M. S. Baker, $n=10$ 370–371

ONAGRACEAE

Cenospecies Zauschneria californica

- Zauschneria cana* Greene, $n=15$ 244
Z. septentrionalis Keck, $n=15$ 244
Z. Garrettii A. Nels., $n=15$ 244
Z. californica Presl, $n=30$ 244

The following subspecies (ecotypes) were investigated: sspp.
typica Keck, *angustifolia* Keck, and *latifolia* (Hook.) Keck;
 also \times “*septcata*.”

Two pentaploids with $2n=ca.$ 75 were found in *Z. californica*
angustifolia.

SCROPHULARIACEAE

The genus *Penstemon*

Subsection *Proceri*

- Penstemon procerus* Dougl., usually diploid, $n=8$ 290–291
 Many diploid forms investigated from Washington, Oregon,
 California, and Utah. They include var. *aberrans* (Jones)
 A. Nels., *P. Tolmiei* Hook., and *P. heterodoxus* Greene.
 Tetraploid forms, $n=16$: One form from North Park, Colo-
 rado, and *P. pratensis* Greene from Nevada.
P. cinicola Keck, $n=16$ 291
P. confertus Dougl., $n=16$ 291

<i>P. globosus</i> (Piper) Pennell & Keck, $n=16$	291
<i>P. aggregatus</i> Pennell, $n=16$	291
<i>P. Rattanii</i> Gray, including ssp. <i>Kleei</i> (Greene) Keck, $n=8$	292
<i>P. minor</i> (Gray) Keck, $n=8$	292
<i>P. ovatus</i> Dougl., $n=8$	292
<i>P. cinereus</i> Piper, $n=8$	291
<i>P. humilis</i> Nutt., $n=8$	291
<i>P. pruinosis</i> Dougl., including <i>P. albertinus</i> Greene, $n=8$	291
<i>P. virens</i> Pennell, $n=8$	292
<i>P. deustus</i> Dougl., $n=8$	292
<i>P. Wilcoxii</i> Rydb., including <i>P. pinetorum</i> Piper, $n=16$	292
<i>P. euglaucus</i> English, $n=24$	292
<i>P. attenuatus</i> Dougl., $n=ca. 24$	292

Section *Erianthera*

<i>Penstemon fruticosus</i> (Pursh) Greene, $n=8$	292
<i>P. Barrettae</i> Gray, $n=8$	292
<i>P. Newberryi</i> Gray, $n=8$	292-293
<i>P. Menziesii</i> Hook. sspp. <i>typica</i> and <i>Davidsonii</i> (Greene) Pennell & Keck, $n=8$	293
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<i>P. rupicola</i> (Piper) Howell, $n=8$	293

Section *Nothochelone*

<i>Penstemon nemorosus</i> (Dougl.) Trautv., $n=15$	293
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Subsection *Glabri*

<i>Penstemon glaber</i> Pursh var. <i>alpinus</i> Gray, $n=8$	293
<i>P. speciosus</i> Dougl., $n=8$	293
<i>P. saxosorum</i> Pennell, $n=8$	293
<i>P. subglaber</i> Rydb., $n=8$	293
<i>P. cyananthus</i> Hook., $n=8$	293
<i>P. strictus</i> Benth., $n=8$	293

Subsection *Coerulei*

<i>Penstemon pachyphyllus</i> Gray ssp. <i>congestus</i> (Jones) Keck, $n=8$	294
<i>P. secundiflorus</i> Benth., $n=8$	294

COMPOSITAE

Achillea millefolium complex

Achillea borealis Bong., $n=27$322-323

The following subspecies were investigated: ssp. *typica* Keck, *arenicola* (Heller) Keck, and *californica* (Poll.) Keck.

A. lanulosa Nutt., $n=18$323

The following ecotypes were investigated: mid-Sierran and Great Basin ecotypes of ssp. *typica* Keck, and subalpine and alpine ecotypes of ssp. *alpicola* (Rydb.) Keck.

A. millefolium L., $n=ca. 27$323

The genus *Artemisia**Artemisia vulgaris* complex

Artemisia Suksdorfii Piper, $n=9$341

A. ludoviciana Nutt., $n=18$341

Spp. *typica* Keck and the alpine *incompta* (Nutt.) Keck were investigated.

One plant of alpine *incompta* was hexaploid, $2n=ca. 54$.

A. Douglasiana Bess., $n=27$341-342

A. Tilesii Ledeb. ssp. *unalaschcensis* (Bess.) Hultén, $n=27$342

A. vulgaris L., $n=8$342

Artemisia tridentata complex

Artemisia Bolanderi Gray, $n=9$349

A. Rothrockii Gray, $n=ca. 36$349

Aster adscendens complex

Aster adscendens Lindl., collective species:

Mid-altitude, subalpine, and alpine forms from the Sierra Nevada, $n=16$. Great Basin form, $n=8$392-393

The genus *Solidago*

Solidago elongata Nutt., $n=9$384

S. multiradiata Nutt., $n=9$384

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